ATTACHED ALGAE AS INDICATORS OF WATER QUALITY IN PHOSPHORUS ENRICHED KOOTENAY LAKE, BRITISH COLUMBIA

by

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ABSTRACT

Kootenay Lake receives high phosphorus loads to its south end and low phosphorus loads to its north end. These loading differences, combined with the lake's 105 km long fjord morphology, should result in a regional trophic gradient in the lake. I studied attached algae to assess how well they supplemented nutrient data in providing a more accurate measure of regional water quality differences. Algal abundance, phosphorus storage, production, species composition and distribution were measured at up to 30 locations in the rocky littoral zone of Kootenay Lake. In addition, physical parameters were measured and water samples were analyzed for major nutrients, anions and cations.

Loadings of total dissolved solids, calcium, and sodium are also highest to the south end of the lake, and concentration gradients of these biologically conservative elements conform to the expected pattern. On the other hand, dissolved and particulate inshore phosphate readings, although high, did not exhibit regional variations.

Attached algae remove large amounts of phosphorus for growth, altering phosphorus concentrations in the lake. Also, attached algae store surplus phosphorus within their cells, more phosphorus being stored in the regions of highest phoshate loadings (over 1.0 μg P mg^{-1} dry weight algae) than elsewhere.

South arm algae had the highest chlorophyll *a* levels, organic weights and production rates. Their results were typical of eutrophic waters. In contrast, north arm algae were less abundant, had lower growth

rates, and were typical of mesotrophic and oligotrophic waters. Eutrophic indicator species, such as the green alga *Cladophora aegagropila* and the diatom *Fragilaria construens*, were abundant in the south half of the lake and generally absent or less common at other locations. Diatom cluster analyses divided the lake into regions, stations in areas of low phosphate loadings forming groups distinct from stations located near high phosphorus inputs.

One must conclude that aqueous phosphorus concentrations, altered by attached algae, are inadequate indicators of Kootenay Lake's trophic gradient. Attached algae do exhibit regional variations consistent with the lake's expected trophic gradient and are therefore good indicators of water quality in phosphorus enriched Kootenay Lake.

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INTRODUCTION

The need for effective water quality measurements has grown with increasing pollution. Although necessary, water chemistry data alone are inadequate. Seasonal or even hourly changes in chemical concentrations combined with the usual practice of spot sampling of relatively few chemical parameters can result in false conclusions about water quality (Ransom & Dorris, 1972). Biological organisms are constantly exposed to the total chemical environment and in this sense are continuous water quality monitors. Biological data supplement chemical data, resulting in better water quality measurements (Patrick, 1949; Cairns, Dickson, and Lanza, 1973). Unfortunately, comprehensive biological investigations of several trophic levels are too time-consuming and costly to be practical in most water monitoring programs.

This study examined a single biological community, the attached algae, and their relationship to water quality. My aim was to assess how well the attached algal data supplemented traditional chemical data to provide a more accurate measure of water quality. It is surprising that attached algae have been so little studied (Wetzel, 1975). Unlike most aquatic organisms attached algae are present in both lakes and rivers and, as primary producers, they occupy an important position in the cultural eutrophication problem.

While basic physical and chemical data were also measured, I extensively examined attached algal nutrient storage, production, abundance and species composition in Kootenay Lake, British Columbia. Kootenay Lake

appeared to be a particularly suitable study area. Pollution from one element, phosphorus, and its effect on several processes within the lake has already been documented by several researchers (reviewed in Northcote, 1973a). Furthermore, the lake's special morphology results in regions of low, high and intermediate nutrient levels (Northcote, 1973a) which should allow an easy assessment of the value of attached algal investigations to water quality studies.

DESCRIPTION OF THE STUDY AREA

Kootenay Lake is a fjord lake filling a north-south trough in the Selkirk Mountains of southeastern British Columbia (Fig. 1). The Kootenay River flows into the south end of the lake. The other major tributary, the Duncan River, enters at the opposite end of the lake, 105 km to the north. The lake drains via the 35 km long, river-like west arm, which arises midway up the lake.

Although surrounded by mountains, only seven percent of the main lake's littoral zone is sheer rock. The remainder has a moderate slope (generally less than 45 degrees) and supports an abundant attached algal flora which grows on boulder-sized pieces of schist or granodiorite. Near the lake's extremities, sediments start at 2-3 m depths, but elsewhere rocks usually predominate to at least 10 m. The west arm shoreline has a much gentler slope than that of the main lake. Substrate in the west arm is usually composed of sand, pebbles, or cobble-sized rocks which, because of frequent shifting, seldom allow a luxuriant algal flora to develop. Infrequent granodiorite boulder outcrops support larger quantities of attached algae.

Although there is little domestic or industrial development along its shores, Kootenay Lake is showing signs of cultural eutrophication (Northcote, 1973a). High phosphate additions reach the south end of the lake via the Kootenay River inlet. Zyblut (1970), Northcote (1972a,b; 1973a,b) and Parker (1972) have documented that, since 1953, a Cominco Ltd. fertilizer plant operating 400 km upstream has significantly contributed to the high

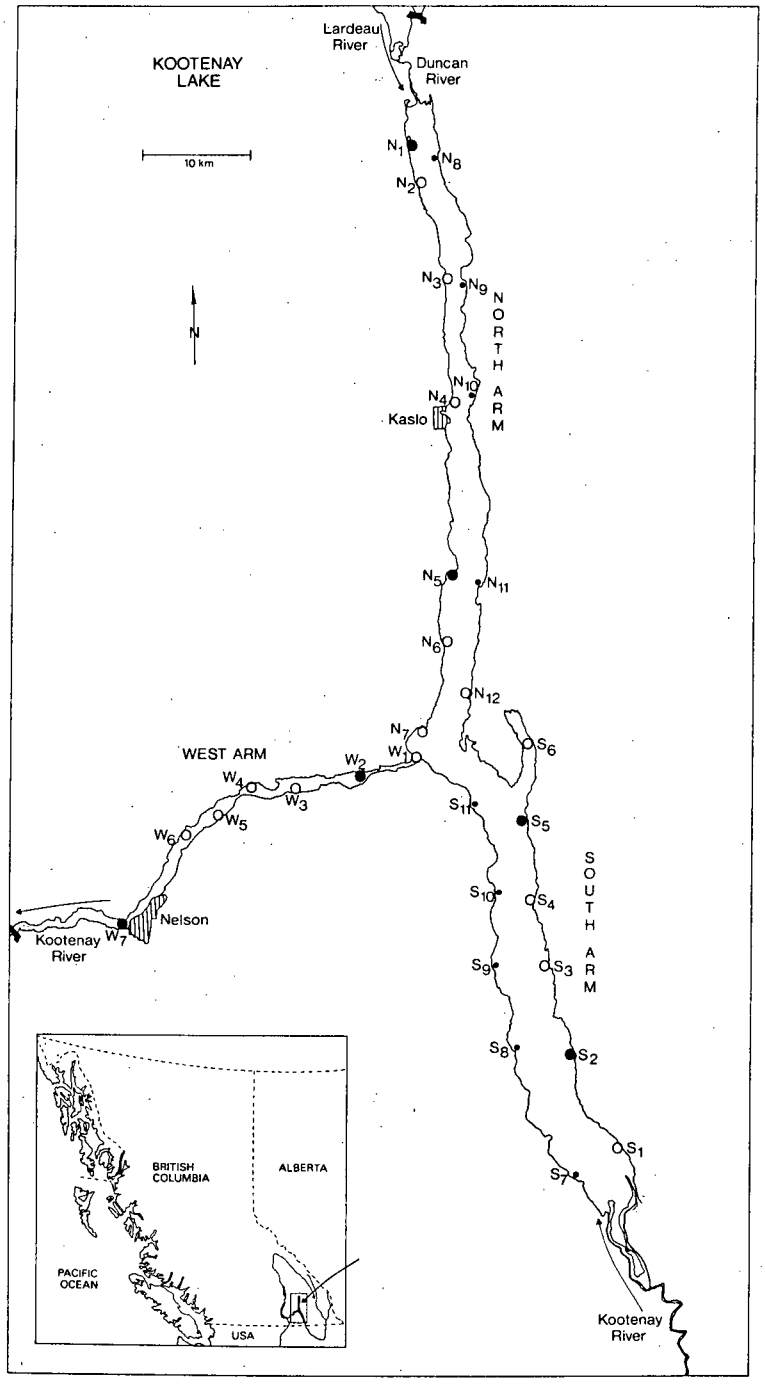
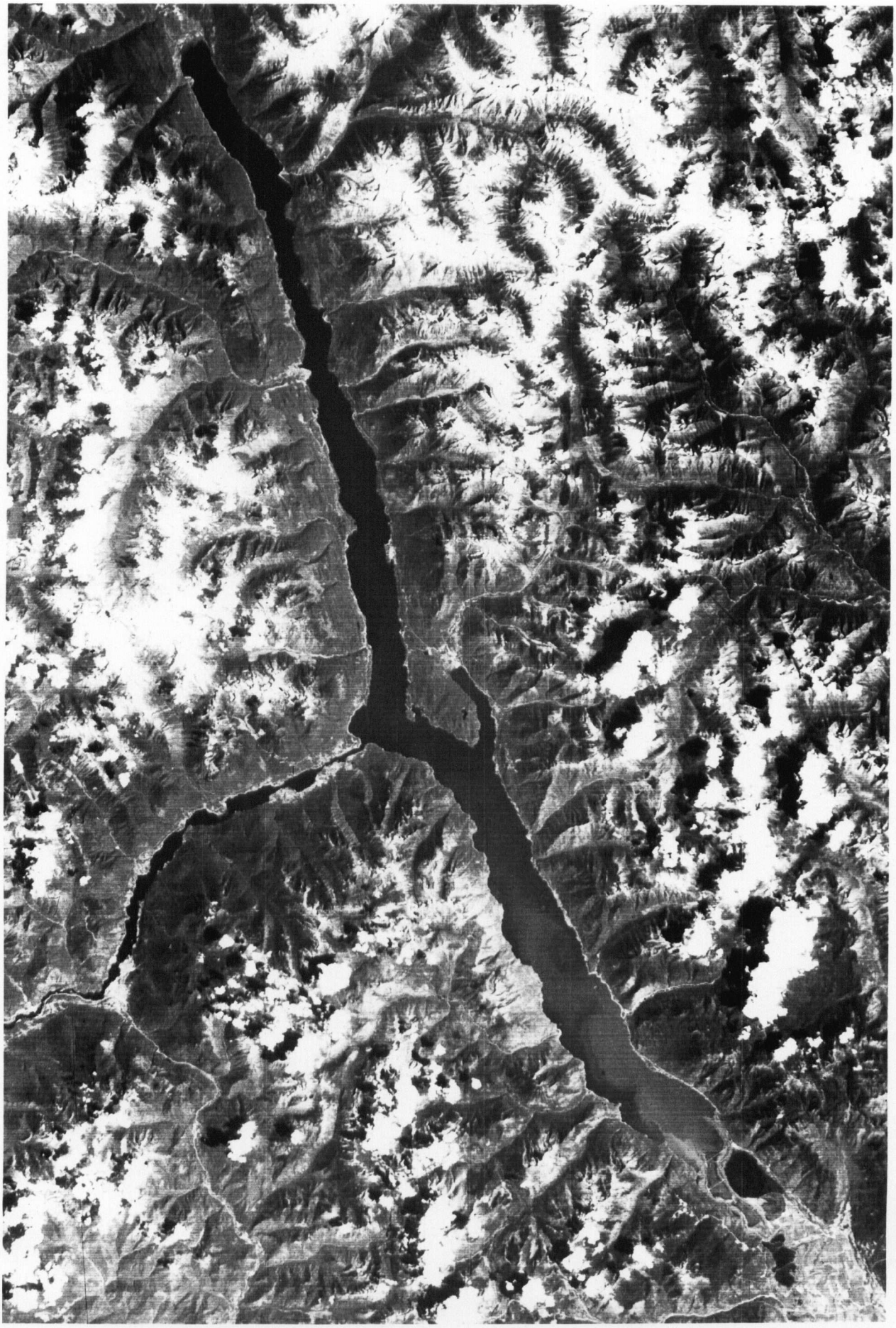


Fig. 1. Kootenay Lake showing the sampling stations on the north, south, and west arms. Main littoral sampling locations are indicated with solid circles, minor sampling locations with open circles, and those locations sampled only once are indicated by dots.

Kootenay River phosphate loads. The impact of the Kootenay River on the south half of Kootenay Lake is dramatically illustrated in Plate 1. The Duncan River, on the other hand, adds comparatively little phosphorus. Since the west arm arises midway between the two rivers, three major lake regions (north 'arm', south 'arm' and west 'arm') with three contrasting nutrient levels (low, high and intermediate) are potentially formed.

Plate 1. LANDSAT satellite imagery (colour bands 4, 5, 7) of Kootenay Lake, 3 August 1974, showing the influence of the Kootenay River inlet on turbidity patterns in the south arm of Kootenay Lake. Original print identification: Cycle 42, Day 1, Track 47, Frame 25, 3/8/74 - available from Integrated Satellite Information Services, Prince Albert, Saskatchewan.



FIELD AND LABORATORY PROCEDURES

Sampling Program

Field work on Kootenay Lake took place once in March, weekly from May until mid-September, and monthly during October, November and December, 1973. In addition, samples were collected during September 1972 to familiarize myself with the research area and relevant field and laboratory methods. During July 1974 I measured some physical parameters on the lake.

For personal safety, while sampling the turbulent main lake, regularly sampled research stations were located near highway access, which was generally only available on one side of the lake or the other. The lake's large size generally necessitated sampling the lake over a three-day period. As far as practicable, north arm stations (N1-N12) were sampled on the first day, south arm stations (S1-S11) on the second day and west arm stations (W1-W7) on the third day. The only exception was station N12 which, because of highway access, was sampled with the south arm stations. Two stations on each major arm of the lake were selected for intensive study. Those stations (N1, N5, S2, S5, W2 and W7--black circles in Fig. 1) were sampled weekly from May until mid-September and once during each of the other months of study. Remaining main lake stations on the highway side of the lake were sampled twice a month from May until mid-September as were all of the remaining west arm stations (open circles in Fig. 1). Once during the study, stations N8 to N11 and S7 to S11 (black dots in Fig. 1), across from regular north and south arm stations, were sampled to determine if conditions were similar on opposite shores of the lake.

Attached algal samples were collected at main research stations from 0.1, 1.0, 3.0, and where possible 5.0 m depths. Occasionally, samples were collected from 10.0 m below the water surface. Those depths were chosen to represent the lake's splash zone as well as regions of high, moderate and low light intensities. Algae were collected from the other stations at only the 1.0 m depth except once a month during the intensive sampling period when they were collected at all four depths.

Physical and chemical measurements were also performed during the algal sampling periods. Temperature profiles from the surface to five meter depths, and Secchi disk readings were taken at all stations. Main station chemical samples were collected weekly from the 1.0 m depth and once a month from all sampling depths. Water chemistry collections from the 1.0 m depth were made once a month at the minor stations.

Physical Measurements

At each station, water temperature was measured with a YSI Model 54 oxygen meter. Water transparency was measured with a standard Secchi disk, and once during the study subsurface illumination was measured using a Montedoro-Whitney illuminance meter (Model LMT-8B). Daily bright sunshine readings (Atmospheric Environment, 1974) taken at the Castlegar airport (36 km from Nelson) were used to obtain energy input in kcal m^{-2} to the surface waters of Kootenay Lake.

Chemical Measurements

For the purpose of chemical analyses, one-liter polyethylene bottles were filled with lake water lying directly above the algal substrates. Water

samples were frozen and usually analyzed within two months for pH, total dissolved solids, alkalinity, sodium, calcium, phosphate (ortho, total and poly), nitrate nitrogen and silicon dioxide, by Cominco Ltd. at Trail, British Columbia. All analyses were performed as outlined in Standard Methods (American Public Health Association, 1971), or else by modified versions of those methods.

Algal Collections

1. Natural Substrates

Rocks approximately 20 cm in diameter were collected by diving, and sampled quantitatively for attached algal growth. The schist or granodiorite rocks were very similar in chemical composition (Dr. L.H. Green, pers. comm.) and I feel that differences in algal populations cannot be attributed to different rock types. I tested this assumption once by incubating the two different rock types at the same location; both rocks supported almost identical algal species and biomasses. Furthermore, Fox, Odlaug, and Olson (1969), working in western Lake Superior, have also concluded that different rock types do not affect attached algal growth in any way.

A nylon brush sampler made from a modified 50 cc syringe (Stockner & Armstrong, 1971) was used to remove the algae from the rocks. Two samples with a combined area of 13.2 cm^2 were taken from each rock, so that within rock variance was taken into account. Between rock variance was also considered, algae being frequently sampled from two and even three rocks at each location and depth.

2. Artificial Substrates

Artificial substrates with an area of 225 cm^2 were used to measure the production of attached algae in the littoral zone of Kootenay Lake. The retrieval of artificial substrates at selected time periods has long been used to measure algal production, and the literature is extensively reviewed by Cooke (1956), Sládeček & Sládečková (1964), Sládečková (1962), and Wetzel (1975).

There are several possible sources of error in that technique, which I attempted to eliminate. To reduce the substrate's selectivity to organisms, I used plexiglas substrates. Peters (MS 1959), according to King & Ball (1966) and Backhaus (MS 1965) cited in Wetzel (1965), found plexiglas and polyethylene substrates to be non-selective. Glass substrates used by many researchers, besides being easily broken, are selective towards diatoms, as the silica in the glass is a major diatom cell wall constituent. Hohn and Hellerman (1963) even found that the diatoms on glass substrates were not representative of diatoms growing on adjacent natural substrates. Godward (1937) noticed that green algae seldom colonized glass slides and Tippett (1970) found that succession on glass slides differs from that of natural substrates, but Brown and Austin (1971) noted that algae other than diatoms seldom colonized this substrate.

Literature reports are conflicting as to where the artificial substrates should be placed. Many researchers suspend the substrates from lines at mid-lake, but I fail to see how their data could be representative of conditions in the littoral zone. I placed substrates, mounted on 10 kg concrete blocks, on the rocky littoral bottom in horizontal position. This position best represented how natural rock surfaces were aligned (all stations

had a slope of less than 30 degrees). Castenholz (1961) noted that vertical plates supported 6-12 times less material than horizontal plates and that the horizontal plate data very closely duplicated natural attached algal conditions.

The immersion time of the substrates is also an important factor which could be a major source of error. If incubation periods of less than one week are used, settling apparently exaggerates the production rate (Castenholz, 1960). During incubation periods greater than one month, algal competition can seriously affect production rates (Patrick, Hohn, and Wallace, 1954). I therefore incubated and retrieved my plexiglas substrates every two weeks, a time period recommended in the above studies by Castenholz and Patrick et al.

To reduce collection disturbances the substrates were retrieved by diving rather than by pulling up lines or other mechanical methods. As soon as the plates were retrieved, the algae were transferred to a sample jar by use of a razor blade and wash bottle. The algal cells were then immediately preserved with Lugol's solution. Preliminary observations of unpreserved material indicated that the cells were not harmed by this collection method. Observations also confirmed Patrick et al.'s (1954) contention that dead organisms are only rarely observed, since the diatoms are washed off the substrates as they die.

Algal Analytical Procedures

In the laboratory, each attached algal sample was subdivided for biomass determinations, diatom cell counts, and enumeration of the relative

importance of each algal phyla.

1. Biomass

Biomass determinations were performed on every sample by measuring the organic weight of the algae. The organic weight, sometimes referred to as ash-free dry weight or loss on ignition, is the difference between a dry weight (at 60°C) and an ash weight (at 500°C). This procedure effectively weighs only cell contents, not silicified materials such as diatom cell walls or small rock crystals. Chlorophyll a biomass determinations were performed monthly from May until September, using methods outlined in Stockner and Armstrong (1971), and calculated with the SCOR/UNESCO formula given in Strickland and Parsons (1968).

2. Diatom Enumeration

Diatom identification and cell counts were made on subsamples which were incinerated or cleaned in nitric acid (Patrick and Reimer, 1966) and then mounted on microscope slides with Hyrax media. It was impossible to tell if the prepared diatom frustules represented living cells, but preliminary observations of unpreserved material indicated that most cells present in the samples were alive.

To enumerate the diatom frustules on the slide, 36 stratified random fields (Ennis, MS 1972) were counted with a phase contrast microscope at 800 times magnification. This method resulted in a mean of 245 frustules being enumerated per slide. This number is well below the 8000 specimens that Patrick and her co-workers (Patrick et al., 1954) enumerated for their time-

consuming 'detailed readings' but is probably adequate. According to Williams (1964), counts of 300 individuals accurately represent the proportional abundance of the major species. Furthermore, diversity indices such as the Shannon-Wiener function can be reliably calculated with numbers in this range. Patrick (1968) notes that her detailed analysis of community structure is highly correlated with the easier-to-measure Shannon-Wiener function.

Diatom species can differ greatly in size, and therefore diatom species volumes, as well as numbers, are compared in the following sections. Only measurements of Kootenay Lake's diatom species were used to calculate cell volumes, since the literature reports indicate that the same diatom species often differ in size between lakes. For each species, dimensions of ten separate cells were microscopically measured and used to determine average cell measurements for each species. Scaled plasticine models were then constructed, and by comparing water displacements to standards it was possible to establish the species volume. Assuming the models were perfectly made, the precision of the technique was found to be 7 μm^3. Results are therefore presented to the nearest 10 μm^3. The models were not perfect representations of the diatom cells, but I think that even my crudest models would give better results than volumes determined by applying geometric formulae, because diatoms are not perfect geometrical solids but have indentations, projections, etc. The latter can at least be approximated by plasticine models, but not by geometric formulae.

The works of Patrick and Reimer (1966), Cleve-Euler (1951-1955), Hustedt (1930, 1931-1959), Huber-Pestalozzi (1942), Sreenivasa and Duthie

(1973) and Weber (1966) were consulted for identification of the diatoms. Bourrelly's (1968) taxonomic scheme was followed to place the diatoms into orders and where applicable (diatom genera A-M) I followed the species classification outlined by Van Landingham (1967-1971) except that *Cymbella caespitosa* was recognized as a distinct species. For genera not covered by Van Landingham (starting after the genus *Melosira*) I followed, in order of preference, the species taxonomy of Patrick and Reimer (1966), Cleve-Euler (1951-1955), Hustedt (1930) and Huber-Pestalozzi (1942).

3. Community Composition

I measured the relative abundance of each algal phyla in the samples with an inverted microscope using methods detailed in Northcote, Ennis, and Anderson (1975).

In the inverted microscope sample, Cyanophyta and Chlorophyta species were qualitatively measured for relative abundance and identified using Prescott (1962) and Hoek (1963).

Algal Nutrient Analyses

I tested November and December algal samples to see if they stored surplus phosphorus. Stewart and Alexander (1971) demonstrated that, for blue-green algae at least, excess phosphorus is stored in vegetative cells as polyphosphate bodies. These bodies serve as a store of phosphorus for the algae when exogenous phosphorus is limiting. Fitzgerald and Nelson (1966) developed a practical method which I used to extract the surplus stored phosphorus. The results, besides determining whether or not phosphorus is

limiting to growth, can be used to see if one region has more available phosphorus than another region, even if excess phosphorus is present in both systems. The technique involves washing the algae several times in phosphate free water to remove any aqueous phosphorus. The surplus phosphorus is then extracted from the algae in a boiling water bath, and analysed by the stannous chloride reduction procedure outlined in Standard Methods (American Public Health Association, 1971).

Statistical Reliability of the Algal Data

1. Field Collections

By combining two algal subsamples from a single rock, variance of species counts was proven to be significantly reduced (Ennis, 1975). Hence two subsamples per rock were always taken.

In Kootenay Lake attached algal growth is very uniform, and variability between rocks is much less than in most lakes and rivers. Once during the study, at station N1 (3 September 1973, 1.0 m depth) ten different rocks were sampled to statistically examine between rock algal variability. Algal species counts, biomasses, and diatom diversity between rocks was more variable than on a single rock, but not statistically so (Ennis, 1975). Frequent collection of algae from replicate rocks partially compensated for the inherent between rock variability.

2. Algal Enumeration

I had statistically analysed algal enumeration methods using Fraser River attached algae (detailed data in Northcote et al., 1975). Since the Kootenay Lake specimens were prepared by identical methods, I assume that

my previous conclusions still apply as follows. The diatom subsampling procedure was random and diatoms were always evenly dispersed on the microscope slides. Also, subsamples always reliably depicted the diatom species in terms of percentage composition, diversity (Shannon-Wiener function), numbers of species present and transformed cell numbers. Untransformed total counts were not random, although the most extreme deviation between subsamples (23 percent) was well within the acceptable limits suggested by Lund, Kipling and LeCren (1958).

Ten subsamples of Fraser River algae taken to test the reliability of algal phyla composition data, indicated that 20 percent of the time the abundance of green algae would be overestimated. The large error presumably occurs because the green algal filaments tend to become entangled and cannot be completely separated by vigorous shaking. Large green algal filaments are not as common in Kootenay Lake as in the Fraser River, and the possibility of error in the present study is probably considerably less than 20 percent.

Algal Transfer Experiments

To determine how algae growing in one region of Kootenay Lake respond to chemical and physical conditions in other parts of the lake, reciprocal transfer experiments were conducted. Although such a technique seems particularly suited to testing the effects of varying physical and chemical factors on community structure, Parker, Samsel and Prescott (1973) appear to be the only researchers to have previously used such a technique in the study of attached algae.

Eight plexiglass plates were immersed simultaneously at the 1.0 m

depth of stations N1, S2 and W7. At each station, after two weeks' growth, a plate was scraped and the algae preserved for laboratory analysis. One plate was left at the original station and the remaining six plates were transferred, one to each of the other five main stations, plus station S1 near the inlet of the Kootenay River. As a control, uncolonized plates were incubated at all seven stations. After another two weeks' growth, all the plates were removed for laboratory analysis. A pictorial representation of the experimental procedure is presented in Figure 2.

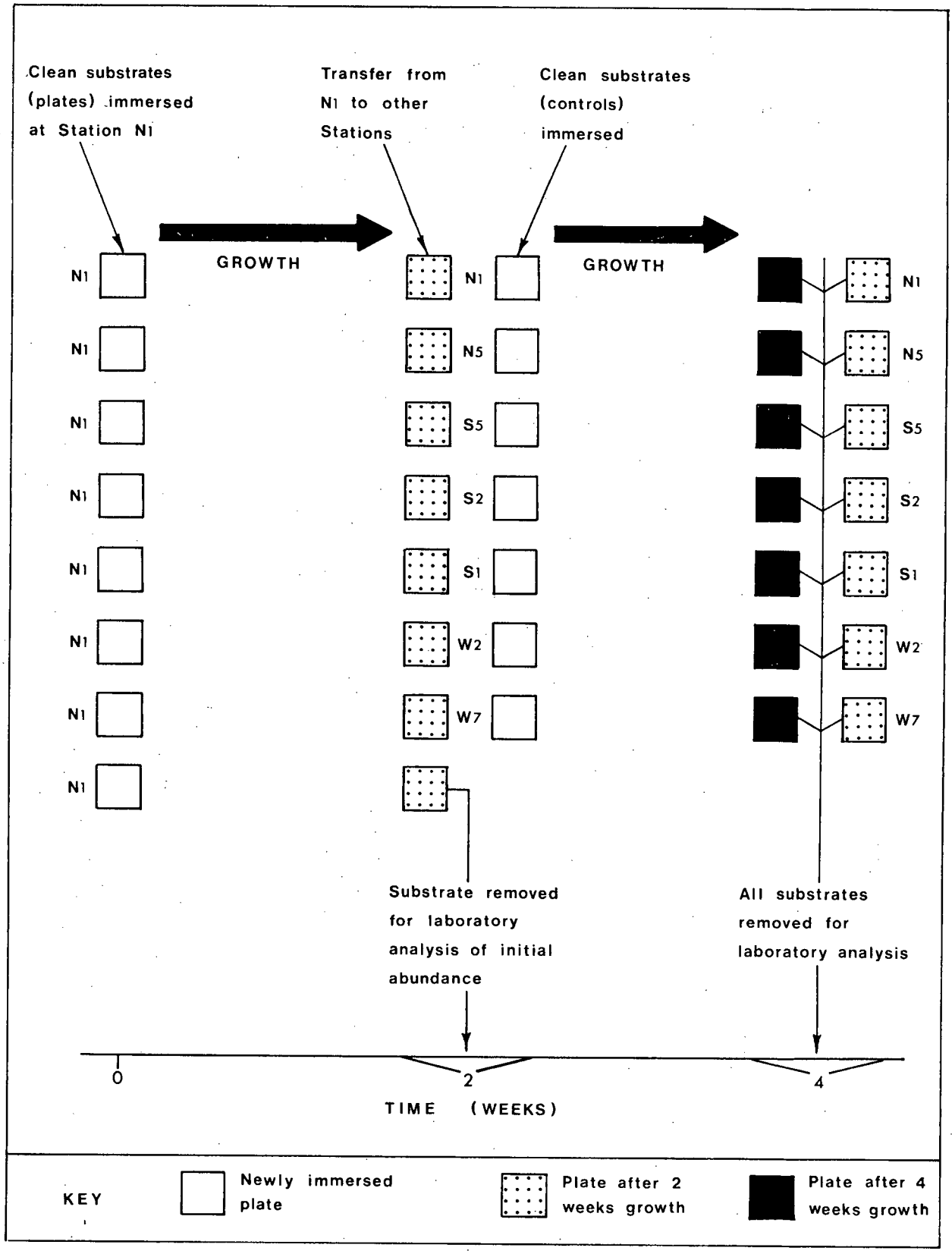


Fig. 2. Pictorial representation showing how the transfer experiments were conducted for station N1. Similar transfers were simultaneously conducted for stations S2 and W7. See text for explanation.

LAKE PHYSICS

Water Input

Over half of the surface water (57.9 percent) entering Kootenay Lake is supplied by the Kootenay River (calculated from Northcote, 1972b). Historical data (since 1928) show that most of this water used to enter during 'spring' freshet, which lasted from April to July but peaked to over 14 m^3 sec^{-1} in May and June (Water Survey of Canada, 1974a; Fig. 3). Since 1972 the Libby dam has regulated the Kootenay River discharge, and during the study year (1973) there were two small but distinct discharge peaks of about 4 m^3 sec^{-1} (Fig. 3). The overall effect of the dam appears to be a more even yearly water discharge into Kootenay Lake. It seems likely that the drastic reduction in normal spring freshet could significantly affect nutrient and turbidity inputs to the lake at the beginning of the algal growing period.

The Duncan River, the other major inlet, supplies 18.5 percent of Kootenay Lake's surface inflow. This inlet has been regulated since 1967, and in 1973 it had a very unusual discharge pattern (Fig. 4A). (For purposes of illustration the Duncan and Kaslo River discharge data are plotted on a more expanded scale than are the Kootenay River data.) There was a winter discharge peak (Dec. 1972-Feb. 1973) of almost 3 m^3 sec^{-1}, an April minimum of less than 0.5 m^3 sec^{-1} and a 'spring' freshet of about 3 m^3 sec^{-1}. After the 'spring' freshet (July-September) the discharge steadily decreased. There are no historical data prior to the Duncan Dam operation to compare with 1973's data, but the winter discharge peak is inexplicable as far as natural water cycles are concerned, and must be related to water regulation. The

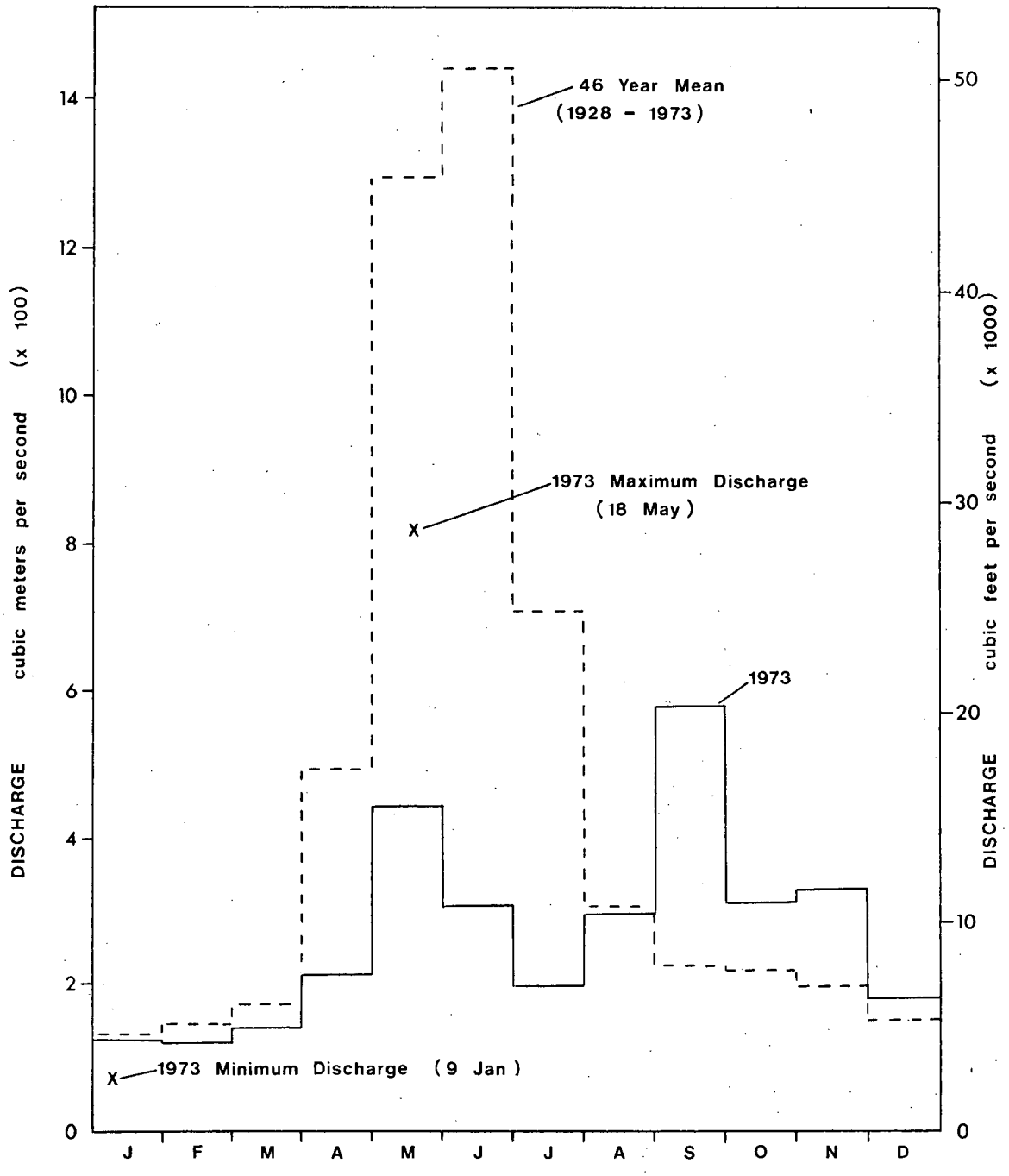


Fig. 3. Average monthly discharges of the Kootenay River at Porthill, 42 km upriver from its inflow to the south end of Kootenay Lake. Solid lines represent 1973 flows, broken lines represent 46 year average flows (1928-1973). Maximum and minimum 1973 discharges are marked. Data from Water Survey of Canada.

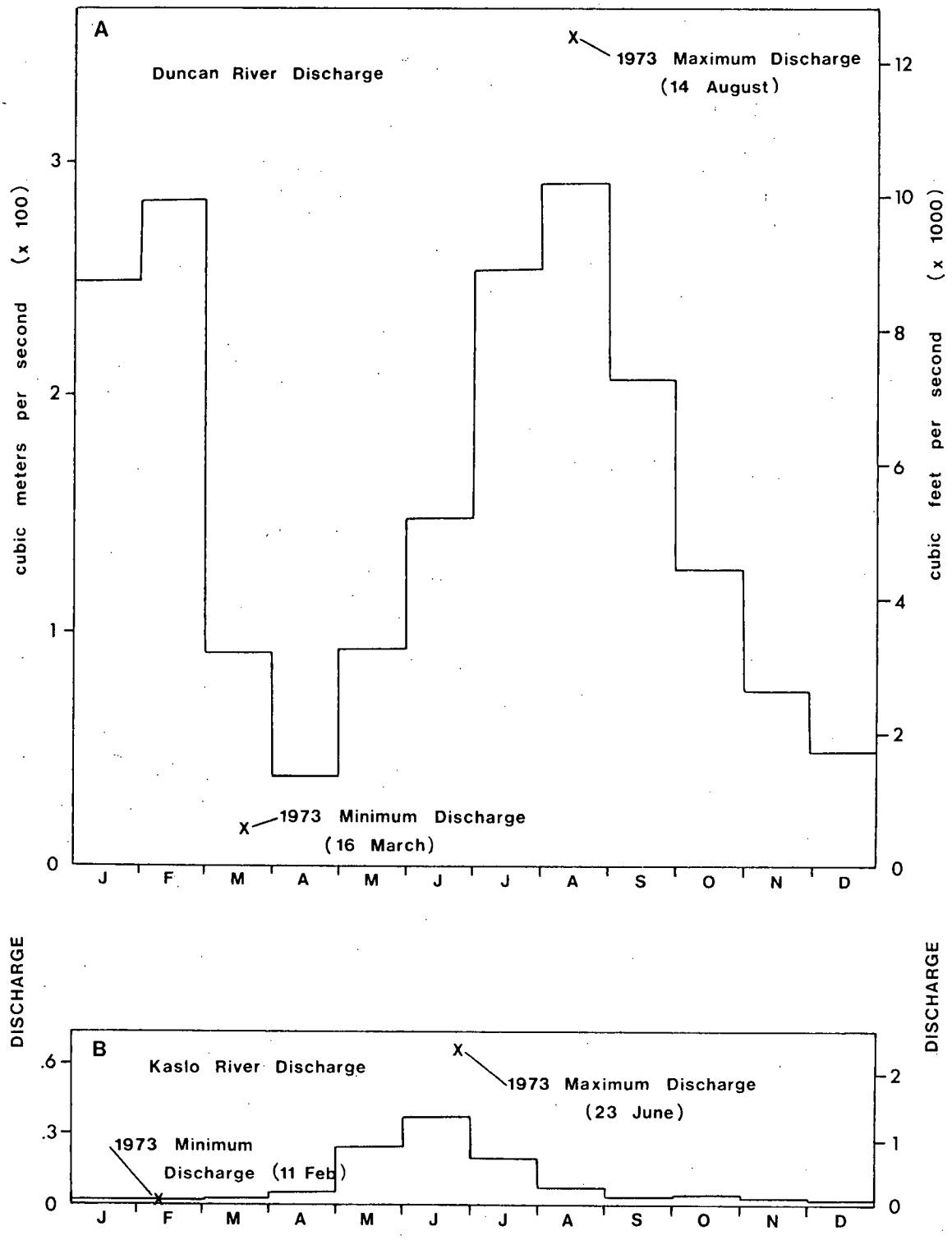


Fig. 4. A-1973 average monthly discharges of the Duncan River, 9 km upriver from its inflow to the north end of Kootenay Lake. B-1973 average monthly discharges of the Kaslo River 5 km upriver from its inflow to Kootenay Lake, just south of station N4. Maximum and minimum discharges are also marked. Data from Water Survey of Canada.

discharge curve for the rest of the year appeared to be normal.

Water inflow from several small tributaries around the lake's margin accounts for 23.6 percent of Kootenay Lake's surface input. Kaslo River, which has a greater discharge than most of the local tributaries, has been chosen to represent lake margin inputs since it is the only small tributary whose flow is monitored year round. Kaslo River's discharge, like that of the other small tributaries, is not regulated by dams. It has a more natural discharge cycle, with almost all the water entering during spring freshet (May-July; Fig. 4B).

Water Level

Water level fluctuation was similar throughout Kootenay Lake, with a 1.95 m difference between the maximum and minimum water levels (Water Survey of Canada, 1974b; Fig. 5). Water levels are lowest during April when discharges into the lake are at a minimum. The lake level increases rapidly in May (1.3 m in a week) corresponding to a large increase in water input with spring freshet. Not all water level changes can be attributed to river inputs though; dams on the lake's outlet have affected water levels since 1938 (Northcote, 1972b). Whatever the cause of water fluctuation, the effects on attached algal populations are the same. Whole populations can be eliminated through exposure, and photosynthesis is greatly affected by altered water, and hence light, levels.

Solar Radiation

The amount of energy entering Kootenay Lake from solar radiation

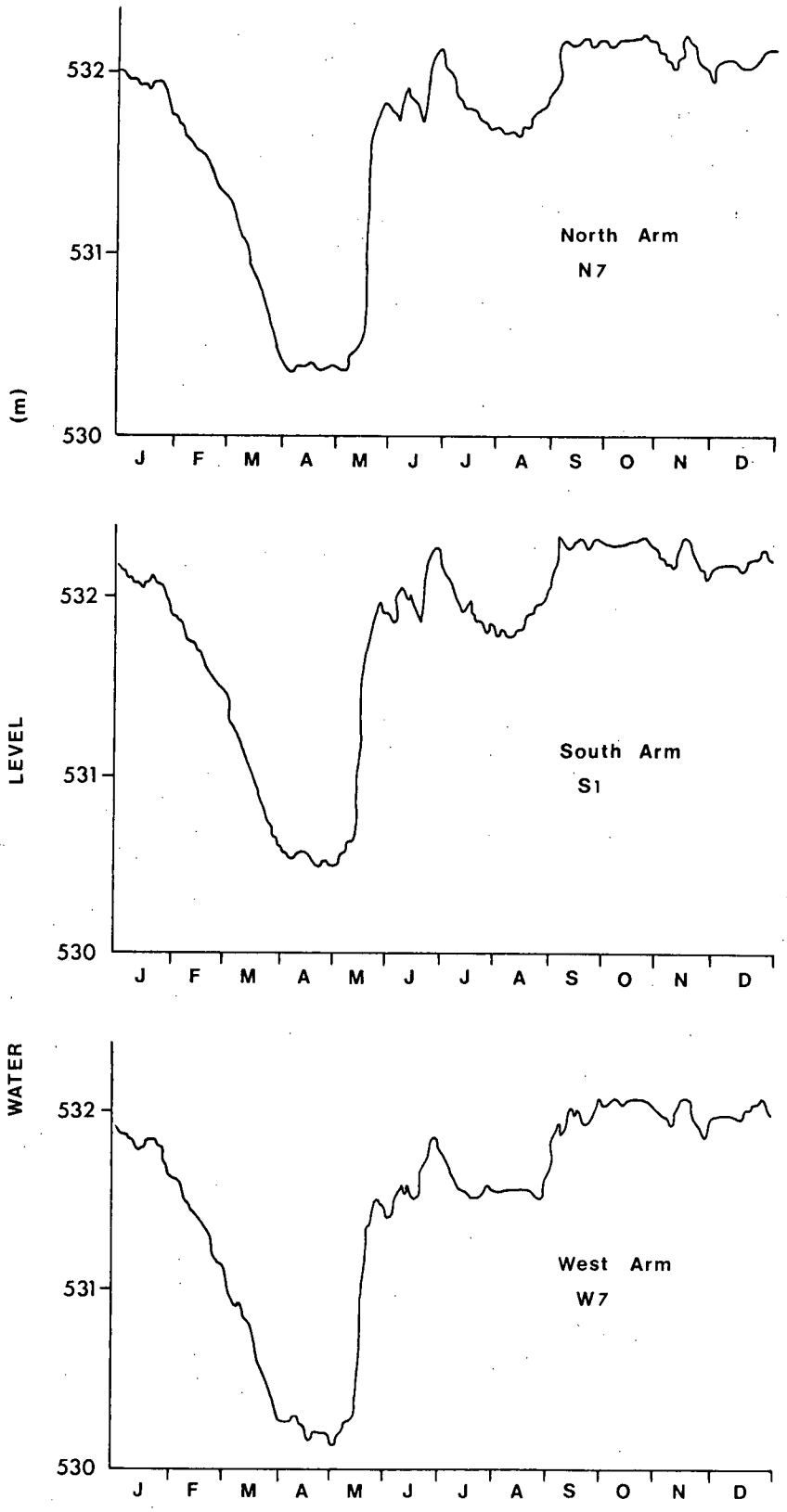


Fig. 5. Water levels (m) during 1973 in the north (station N7), south (station S1), and west (station W7) arms of Kootenay Lake. Data from Water Survey of Canada.

was not measured directly. However, 388 direct energy measurements from the mid 1960's (D.B. Fillian, unpublished) were compared to sunshine data collected simultaneously at nearby Castlegar airport (Atmospheric Environment data) and a significant regression resulted (Fig. 6). Transformation of the data produced the best relationship, described by the following formula:

$$\text{square root gm cal per cm}^2 = 13.01 + (0.9211 \times \text{daily bright sunshine \{hrs\}}).$$

Therefore, 1973 sunshine data (Atmospheric Environment, 1974) were used with the regression equation to estimate energy input to the lake. These data are not formally presented but were used in multiple regression analyses to account for differences in attached algal populations.

Subsurface Illumination

The illumination at depths where algal populations were collected, and the compensation depths (below which primary producers cannot survive) were seldom measured directly. Secchi disk readings, used to measure Kootenay Lake's transparency, do not provide sufficient information on these factors. During July 1974 I measured the compensation depth, defined as the depth at which there is only one percent of the surface light, directly with an underwater light meter. By using this and similar data collected during 1972-1974 by the B.C. Pollution Control Branch (unpublished), I was able to establish a relationship between Secchi disk transparency and the compensation depth (Fig. 7A). A $\log_{10}$ transformation of the Secchi data resulted in a highly significant regression (Fig. 7B) which is described by the following equation:

$$1\% \text{ surface light} = 1.318 + (19.63 \times \log_{10} \text{Secchi depth})$$

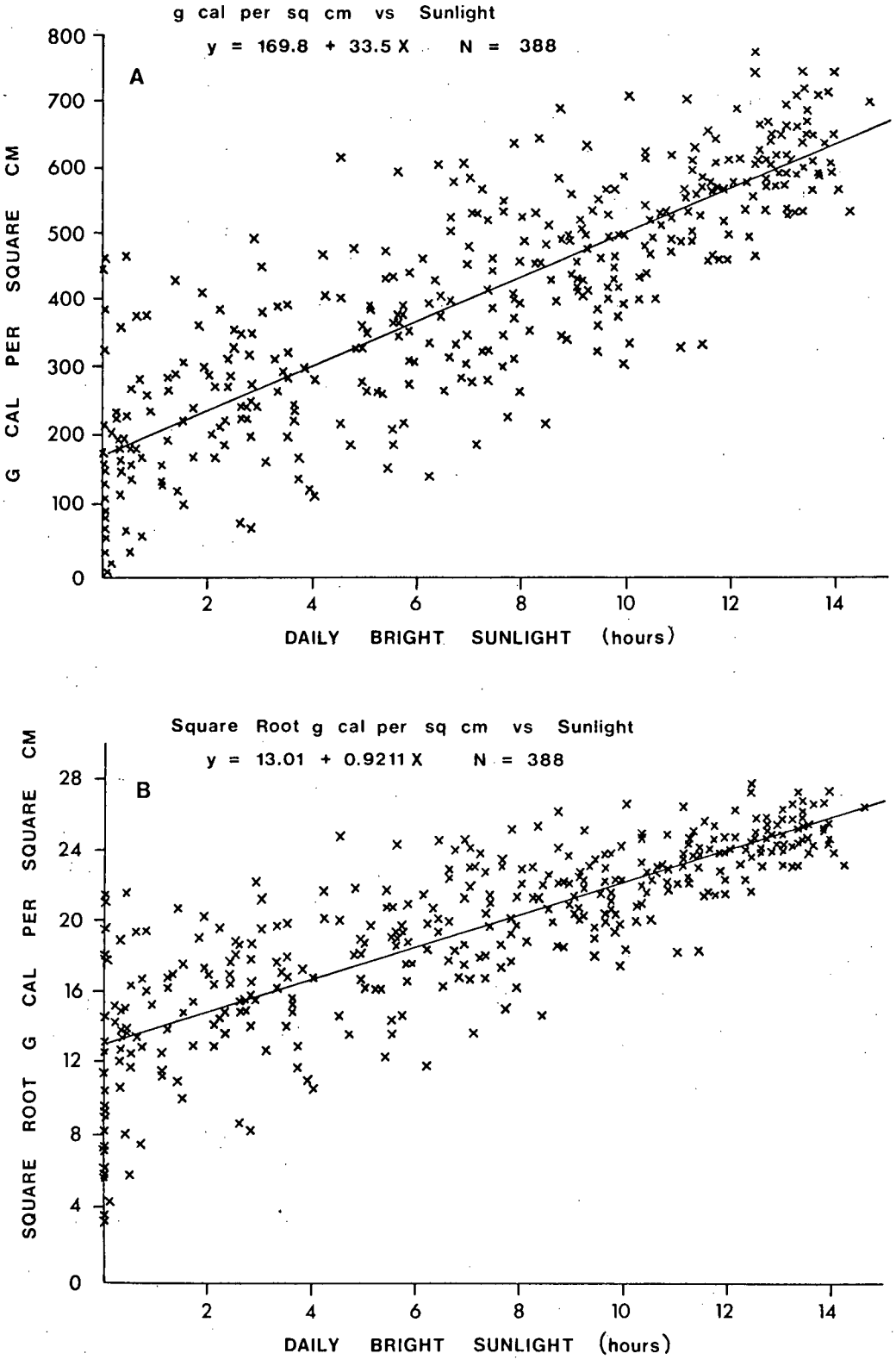


Fig. 6. Relationship between sunshine at Castlegar airport and energy input to Kootenay Lake, 1964-1966. A--untransformed data. B--square root transformed to reduce variance. Sunshine data from Atmospheric Environment, energy input data collected by Mr. D. B. Fillian.

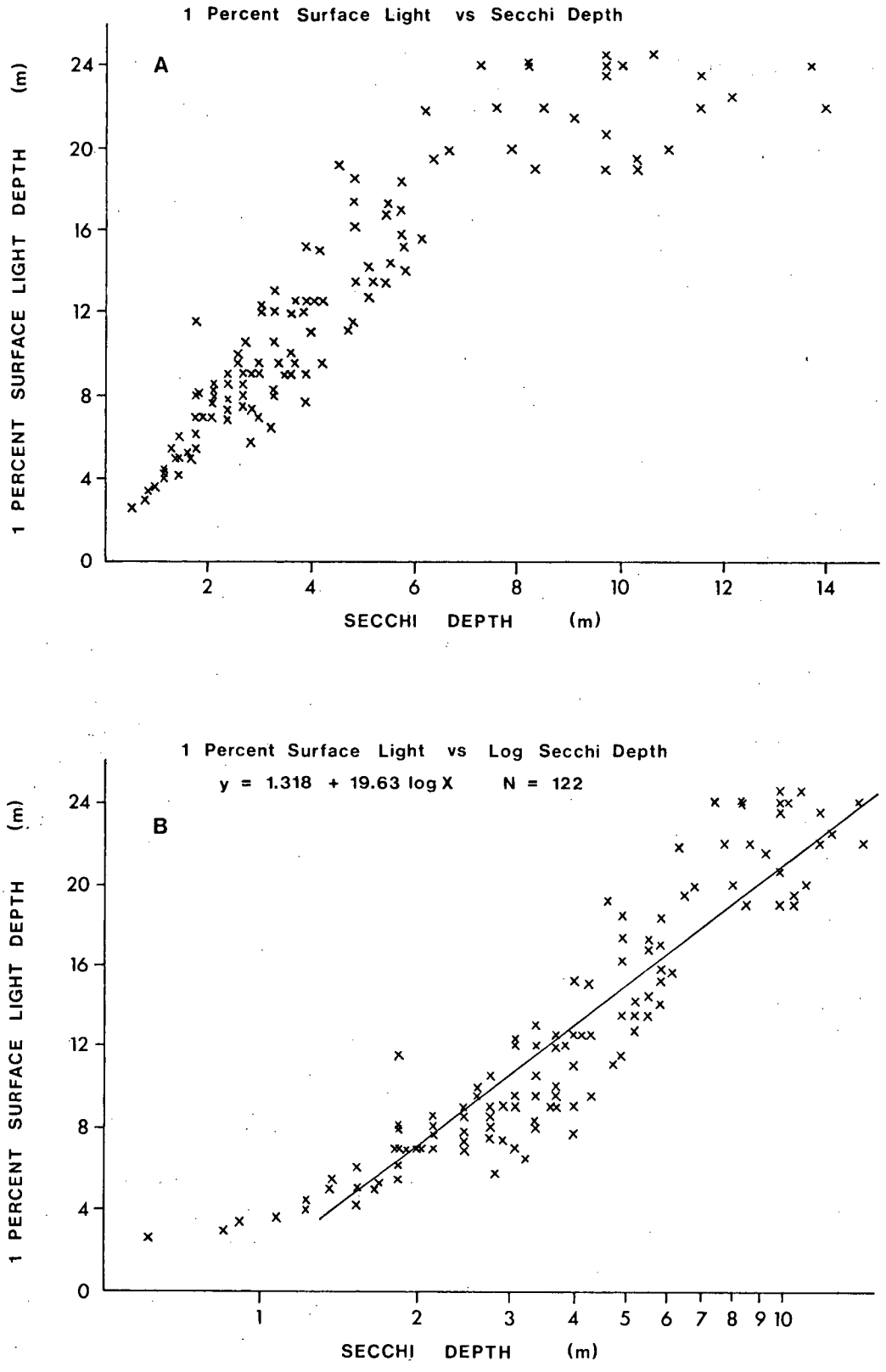


Fig. 7. Relationship between Secchi depth and the depth at which only one percent of the surface light remains in Kootenay Lake, 1972-1974. A--linear scale. B--logarithmic scale. Some data from B.C. Pollution Control Branch.

As a general rule, when using the formula, the compensation depth was about three times the Secchi depth.

Light intensity drops logarithmically with depth and is described by the following classical equation:

$$I_z = I_0 e^{-kz}$$

where I_0 is the irradiance just beneath the water surface (100%), k is an extinction coefficient and z is any depth below the water surface. Since I_0 and the 1% illumination (I_z) depth (z) are known, I can solve for the extinction coefficient k (which is merely the slope of the logarithmic curve between the surface and compensation depth see Fig. 8B). Once the extinction coefficient is known, I can estimate the amount of light (I_z) at any desired depth (z). This procedure is similar to the reasoning of Poole and Atkins (1929) and Idso and Gilbert (1974), except that k, the extinction coefficient, is calculated from empirical Kootenay Lake data and not from general assumptions. The relationship between a direct light extinction plot, a logarithmic plot of the data, Poole and Atkins' estimate, and my estimate is illustrated graphically in Figure 8. By multiplying the surface energy (solar radiation determined above) by the amount of subsurface illumination, I was able to obtain the energy available for photosynthesis at any given depth. In later sections I relate this available energy to the attached algal populations.

Secchi Disk Transparency

Inshore water transparency, measured with a Secchi disk, was lowest at the main lake's extremities where turbid water from the major

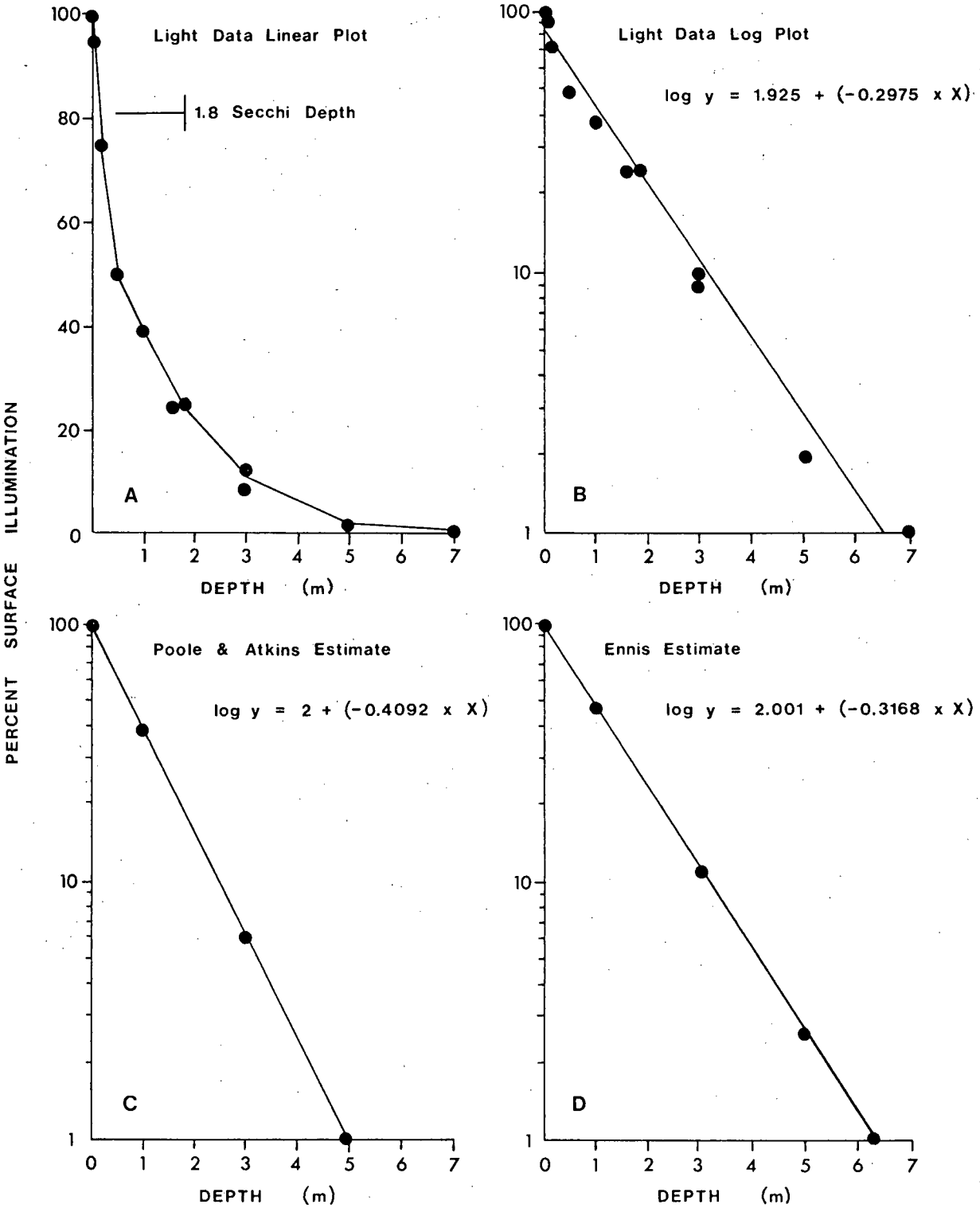


Fig. 8. A comparison of measured versus calculated subsurface illumination for station S5, 4 July 1974. A--measured data plotted linearily. B--measured data plotted logarithmically. C--Poole and Atkins (1928) estimate based upon the Secchi depth. D--Ennis estimate based upon the Secchi depth (see text for details). k is the extinction coefficient (slope of the curve), 8B is the actual extinction coefficient, 8C and 8D are calculated coefficients.

inlets enters the system. Transparency was greatest near the confluence of the lake's three arms where most of the suspended sediments had settled out. The north end of the lake was consistently clearer than the south end, with mean summer Secchi depths generally greater than 5 m in the north and generally less than 5 m in the south. The influence of the Kootenay River's sediment input on the transparency of the lake's entire south arm is illustrated in Plate 1. The west arm, which receives its water from the clearest part of the main lake, showed high transparency at its origin. Transparency decreased towards the outlet as several small streams increased the west arm's suspended sediment load.

Seasonal changes in transparency were great and largely a result of changes in river runoff. During early spring, before freshet (Fig. 3, 4), lake transparency was greatest, sometimes over 11 m (Fig. 9a, 10). Near the start of freshet, the lowest Secchi depth readings were generally recorded, being less than 2 m near the major inlets (Fig. 10). During this period rivers were at their most turbid state, as a result of the erosion from the first snow melt. After the initial freshet, the lake gradually cleared (Fig. 10) and mean summer Secchi depths were often between 5-6 m (Fig. 9b). Increased light penetration could no doubt enhance algal photosynthesis and in fact, during late July-early August, a planktonic blue-green alga *(Anabaena)* became so abundant in the south arm as to decrease the transparency there (Fig. 10b; compare with the north arm, Fig. 10a). After the algal bloom, transparency again became similar throughout the entire lake (Fig. 10). During winter 1973 the transparency increased, and was consistently high at all stations with a lake mean of 7.22 m (B.C. Pollution Control Branch data, unpublished).

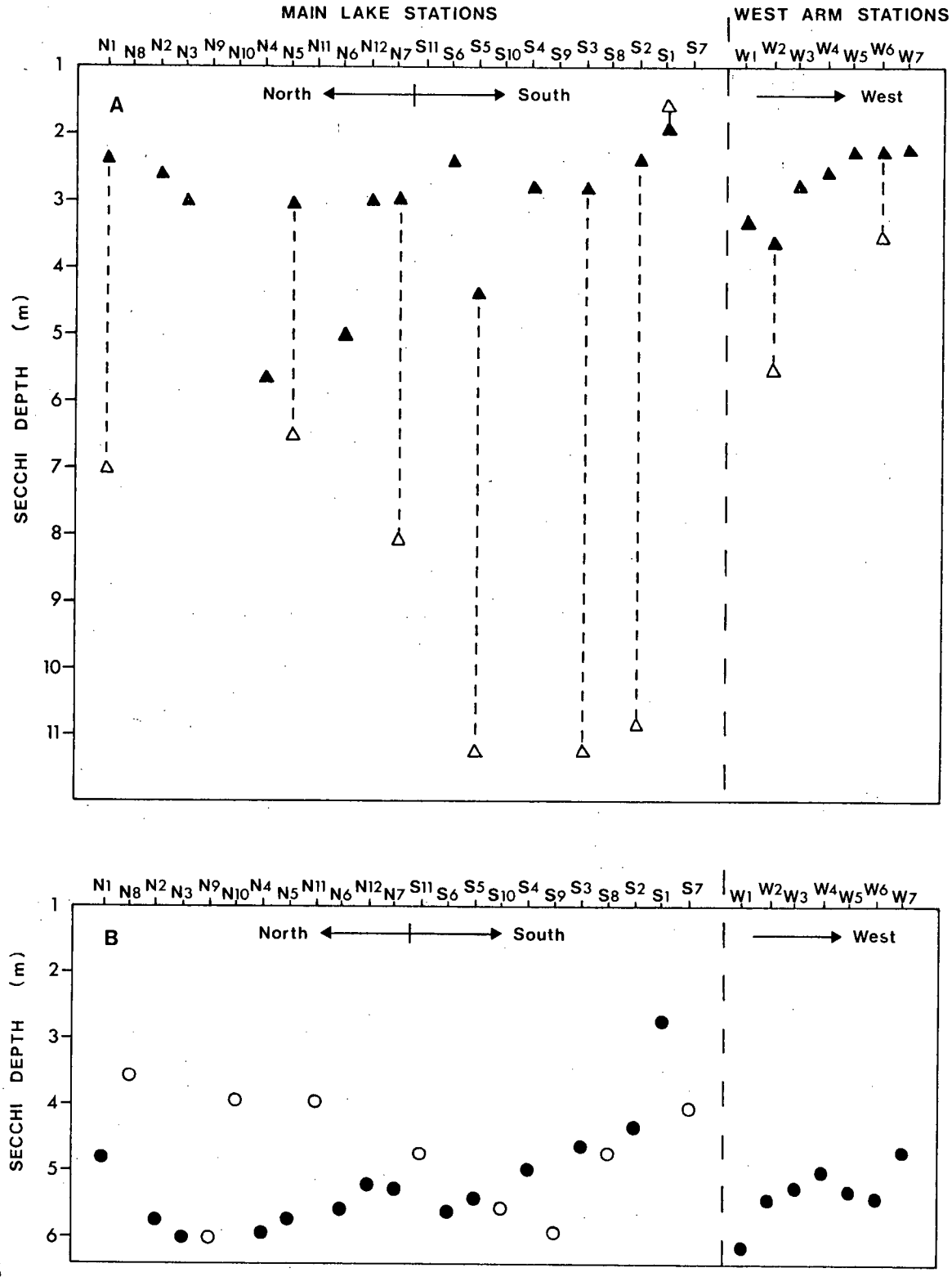


Fig. 9. Regional variations in Secchi disk transparency of inshore Kootenay Lake Water, 1973. A--spring readings; solid triangles represent average values during freshet, open triangles represent single measurements made before freshet. B--summer readings; solid circles represent seasonal average, open circles represent single samples in early July.

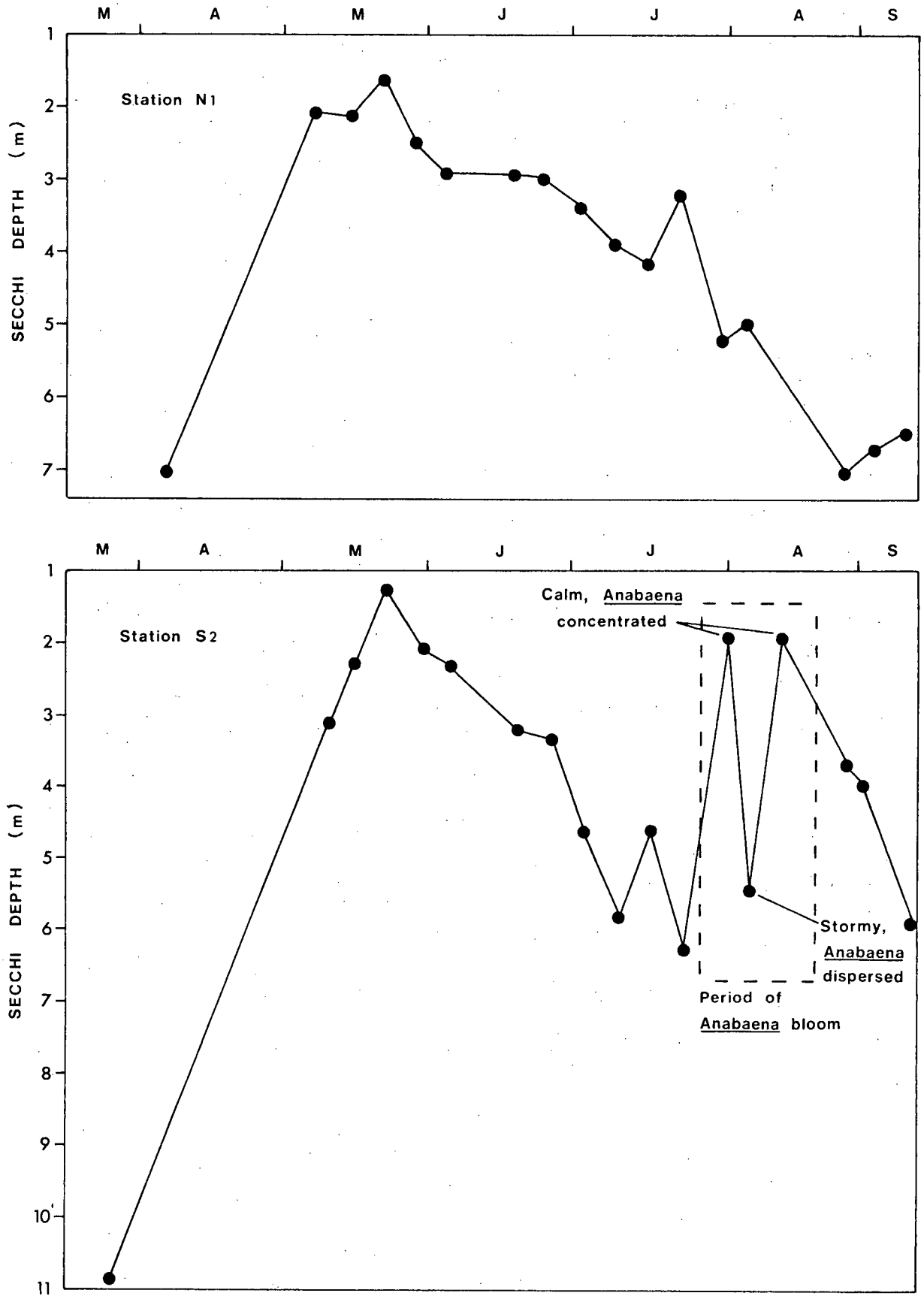


Fig. 10. Seasonal changes of inshore Secchi disk transparency in the north arm (station N1) and south arm (station S2) of Kootenay Lake, 1973.

Both the spatial and seasonal trends in Kootenay Lake's transparency are similar to earlier data reported by Zyblut (MS 1967) and Northcote (1973a).

Kootenay Lake is more transparent than most other lake types (i.e., Wisconsin lakes, Hutchinson, 1957) during winter and early spring, but is characteristically quite turbid during early summer. Summer transparency was greatest in 1949 before industrial activity in the lake's drainage basin (Zyblut, MS 1967; Northcote, 1973a). In the 1960's summer transparency decreased from earlier values, especially in the south end of the lake. Northcote (1973a) believes that even though nutrients were more plentiful there, planktonic photosynthesis was suppressed because of greater turbidity. Light often limits other phytoplankton assemblages and Pieczyńska and Straškraba (1969) found light to also be a dominant limiting factor for attached algal growth. The recent regulation of the Kootenay River by the Libby dam which acts as a partial sediment trap, and the subsequent reduction in the turbid spring freshet (Fig. 3), probably account for greater summer water clarity now than in the 1960's. This clearer water and the subsequent planktonic blue-green algal *(Anabaena)* bloom during 1973 add support to Northcote's theory that primary production at the south end of the lake was light limited.

Water Temperature

Kootenay Lake is a first class, temperate, monomictic lake, stratified from June to October and isothermal for the remainder of the year (Zyblut, 1970). Strong wind action and the consequent mixing of water prevents

the lake from freezing during the winter. The lake's thermal profile has been described in detail elsewhere (Zyblut, MS 1967) and I therefore only measured temperatures in the upper epilimnion (0-5 m) where algal collections were made.

Temperature differences in the upper waters were slight, with usually only a 1-2°C difference between the surface and five meters. Consequently, only data from the 1 m depth is presented (Fig. 11). Occasionally, during calm sunny periods in the summer, as much as a 7°C difference did occur (i.e., 3 Aug. 1973, Station S1; surface - 27.1°C, 5 m - 19.8°C) but such stratification did not persist during windy weather when the epilimnion again began mixing. The upper part of the river-like west arm was almost always isothermal, as was observed in previous years by Zyblut (MS, 1967).

Temperatures were lowest in the north end of Kootenay Lake, highest in the south end, and intermediate in the west arm (see Fig. 11 for representative data). These regional temperature differences were also present in earlier years (Zyblut, MS 1967). Differences in temperature between lake regions were usually less than 5°C however, and all regions showed the same yearly trends (Fig. 11). Spring temperatures gradually rose from near 4°C to approximately 20°C in mid-August, and then gradually decreased to December temperatures of just above 4°C (Fig. 11).

Currents

Attached algal populations are greatly affected by current-carried nutrients, turbidity and even sloughed off algae. A brief report by MacKay (1951) on temperature inferred current patterns in 1950-1951, documented the overriding influence of the lake's largest inlets, the Duncan and Kootenay

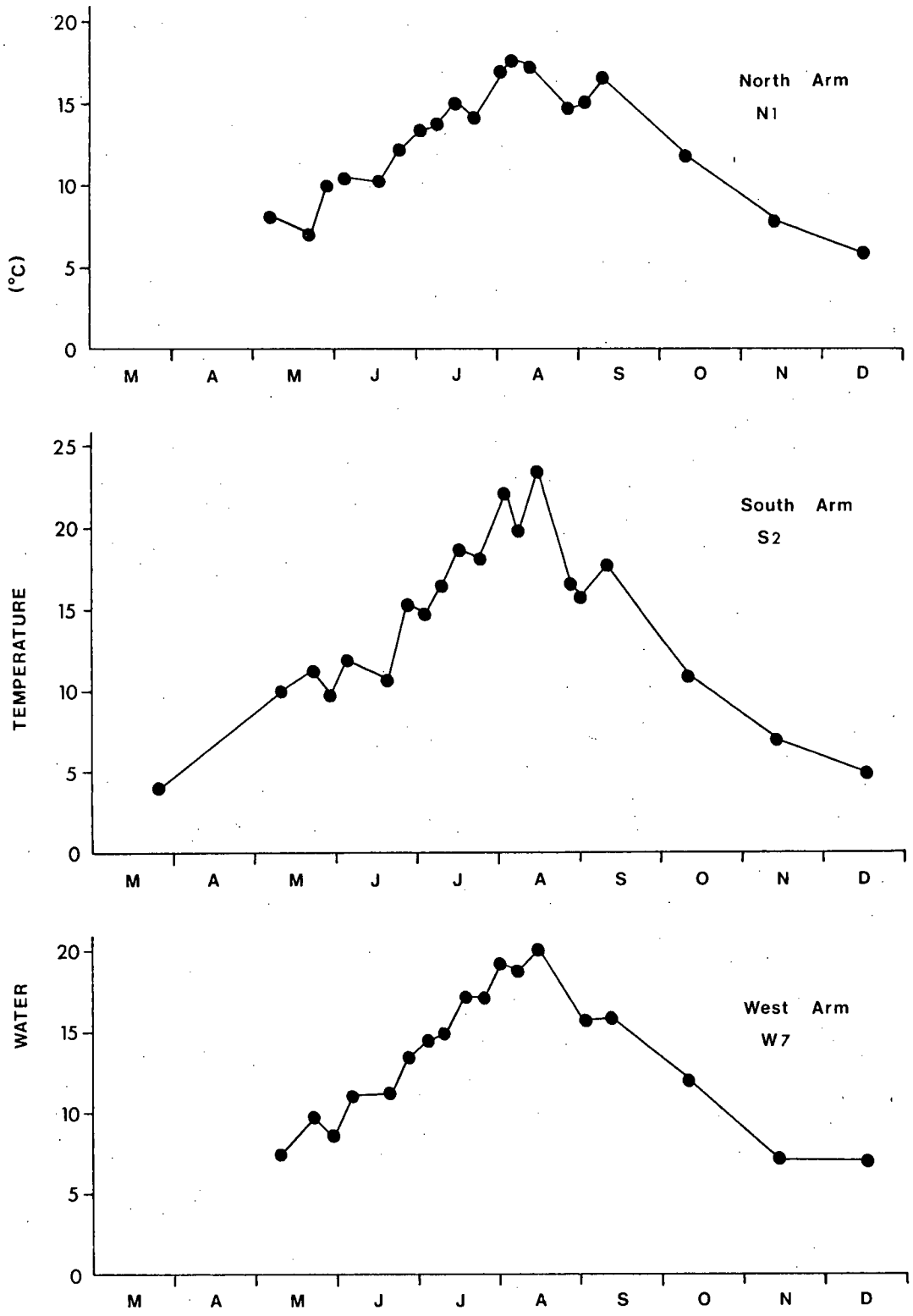


Fig. 11. Temperature (^{o}C) fluctuations of 1.0 m deep inshore water at representative stations in the north arm (N1), south arm (S2), and west arm (W7) of Kootenay Lake, 1973.

Rivers, on lake currents. Unfortunately, major details of the actual currents are not given in that report. Subsequent river regulation by the Duncan and Libby dams may, at any rate, have changed recent currents from those measured by MacKay. Indirect data, such as the turbidity patterns in Plate 1, do however indicate that the major inlets are still an important factor in determining current patterns.

In contrast to the main lake the river-like west arm of Kootenay Lake had noticeable currents flowing towards the lake outlet. This is not surprising since Northcote (1973a) calculated the west arm's yearly mean renewal time to be 5.5 days, with a renewal time of only 1.6 days during June. At station W1 near the start of the arm I measured current speeds of 10 m per minute (29 August 1973). In the wider portions of the west arm currents decreased, but in narrower sections the lake again resumed its lotic tendencies.

LAKE CHEMISTRY

Nutrient Loading

Few wastes discharge directly into the main basin of Kootenay Lake. Considering the basin's large size, relatively high turnover rate (1.5 years; Northcote, 1973b), and few inhabitants (only 800 in the largest town; Ennis, 1975), sewage inputs are insignificant. There are few industries on the lake, and very little agriculture on its mountainous shores (Northcote, 1972a). A currently non-operative mine and smelter at Riondel could have, in the past, added small quantities of sulphates and other materials (Northcote, 1973a).

In contrast to local waste effluents, nutrient inputs from rivers are important. Kootenay Lake's drainage basin is immense, covering an area of over 45,000 km^2, more than a hundred times the lake's surface area. Even before European colonization, nutrient loads from the drainage basin entering the lake via the main tributary (the Kootenay River) must have been high. Northcote (1973 a, 1973b) calculates that prior to the industrialization of the Kootenay basin, phosphorus loading to the lake was approaching Vollenweider's (1971) danger level for producing algal blooms, whereas nitrogen loads were not close to critical concentrations.

In 1953, Cominco Ltd. began operating a fertilizer plant 400 km up the Kootenay River inlet (Zyblut, 1970). Phosphate, lost in the extraction process, entered tributaries to the Kootenay River and in peak years increased phosphate loadings to the lake by over 8,000 metric tons (Northcote, 1972a,b; 1973a). This 'extra' phosphorus caused loads to Kootenay Lake to exceed

Vollenweider's (1971) critical level (Fig. 12). Loads also exceed critical levels determined from more refined models which account for lake flushing rates in addition to mean depths (symbol Ko, Fig. 2 in Vollenweider and Dillon, 1974). Northcote (1973a) describes some biological effects of the eutrophication with respect to the nutrient loadings. In recent years 'extra' phosphate loadings have decreased to 1455 metric tons per year, but total inputs to the lake are still above critical levels.

Nitrate loadings to the lake have not been greatly increased by industrialization. Loadings have been relatively constant throughout the years and well below levels which lead to excessive algal growths (Northcote, 1973a,b; Fig. 12).

The west arm of Kootenay Lake, with an average water retention time of only 5.5 days, is essentially different from Kootenay's main basin and loadings must be treated differently. The region has more inhabitants, and local sewage inputs could be more important than in the main lake. Nelson, just above the lake's outlet, has several small industries including a sawmill and railyards, and industrial waste dumpings into the lake could have deleterious effects on organisms near the city. These local nutrient inputs combined with inputs from the main lake result in high annual phosphorus loadings to the west arm ($> 14\ g\ m^{-2}$), especially when expressed per unit area (since the west arm is much smaller in area than the main lake). Although the short retention time in the west arm may ameliorate the consequences of high nutrient loadings (Northcote, 1972b), annual inputs do exceed the dangerous value of $6\ g\ m^{-2}$ determined from models which include this retention factor (Vollenweider and Dillon, 1974).

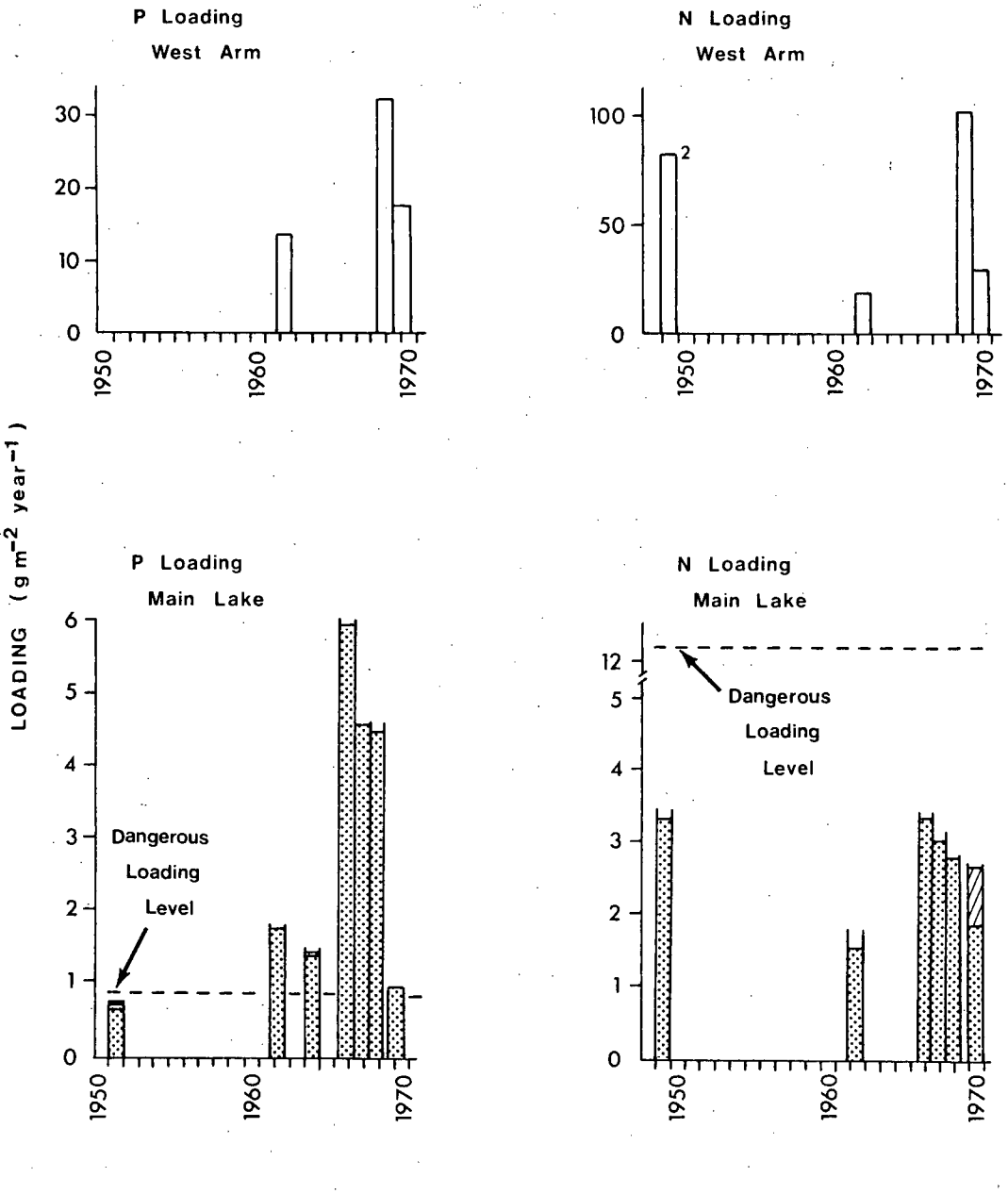


Fig. 12. Approximate annual loading levels for phosphorus (reactive orthophosphate expressed as P) and nitrogen (total nitrate expressed as N) related to unit surface area of the two major basins of Kootenay Lake, 1949-1970's. Stippled portion of bars represent contribution from Kootenay River, shaded portion from Duncan River (excluding Lardeau River for N), solid portion from lateral lake margin. Redrawn from Northcote (1972b).

Phosphorus

Not surprisingly, considering the increased phosphorus loadings to Kootenay Lake, that nutrient has shown an increase since the 1950's. Orthophosphate, the phosphorus compound directly assimilable by algae (McCarty, 1970), has shown over a 50 fold increase (Northcote, 1973a). Concentrations were approximately 0.001 mg l^{-1} in 1949/1950, but in the late 1960's dissolved orthophosphate values tended to fall in the 0.05 mg l^{-1} range. These levels exceeded the critical concentration of 0.01 mg P l^{-1} at which algal problems can develop (Vollenweider, 1971; Dillon and Rigler, 1975). Davis (MS 1973) claims there has been a great reduction in Kootenay Lake's phosphorus concentrations since 1969 and that the lake is oligotrophic; my data and B.C. Pollution Control Branch data do not support his contention. Water samples from the 1.0 m depth analyzed as a part of this study, generally had concentrations of 0.02-0.03 mg l^{-1} of dissolved orthophosphorus, but samples collected during spring freshet were usually over 0.05 mg l^{-1} with some samples having concentrations as high as 0.18 mg l^{-1} (Fig. 13). (Chemistry data for all parameters examined and all samples collected are stored on computer tape, available from the Institute of Animal Resource Ecology, Biological Data Centre at the University of British Columbia.)

As mentioned previously, most of the phosphorus load to Kootenay Lake enters via the Kootenay River at the south end of the lake. The highest dissolved phosphate value (0.18 mg l^{-1}) was recorded in the south end of the lake. Surprisingly though, levels of dissolved, total dissolved and total insoluble phosphate were not consistently higher at the south end of the lake (Fig. 13, 14, 15). Data presented in Figures 13-22 usually represents seasonal means which could obscure the gradient, yet even for single samples

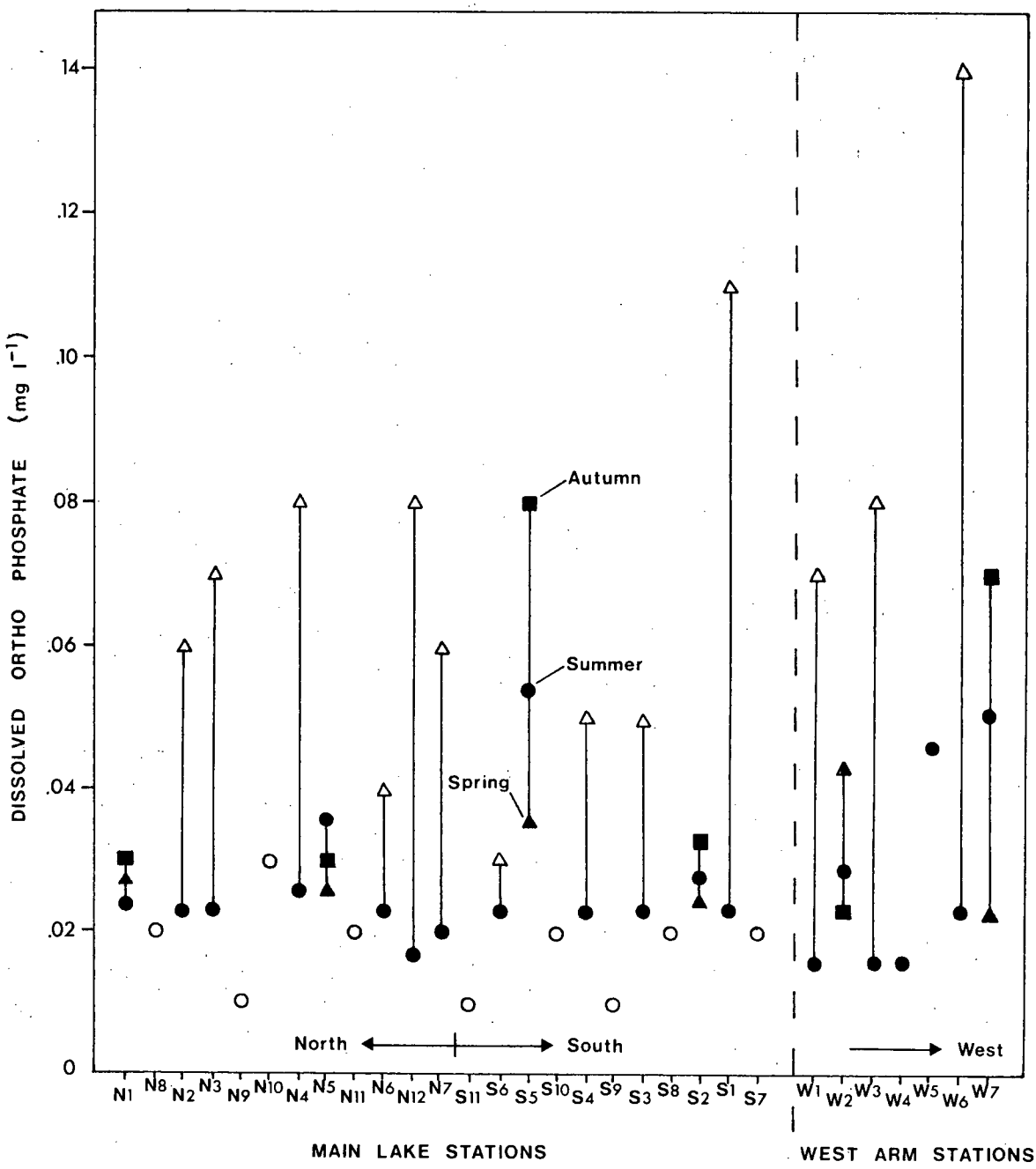


Fig. 13. Regional variations in dissolved orthophosphate (as P) content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

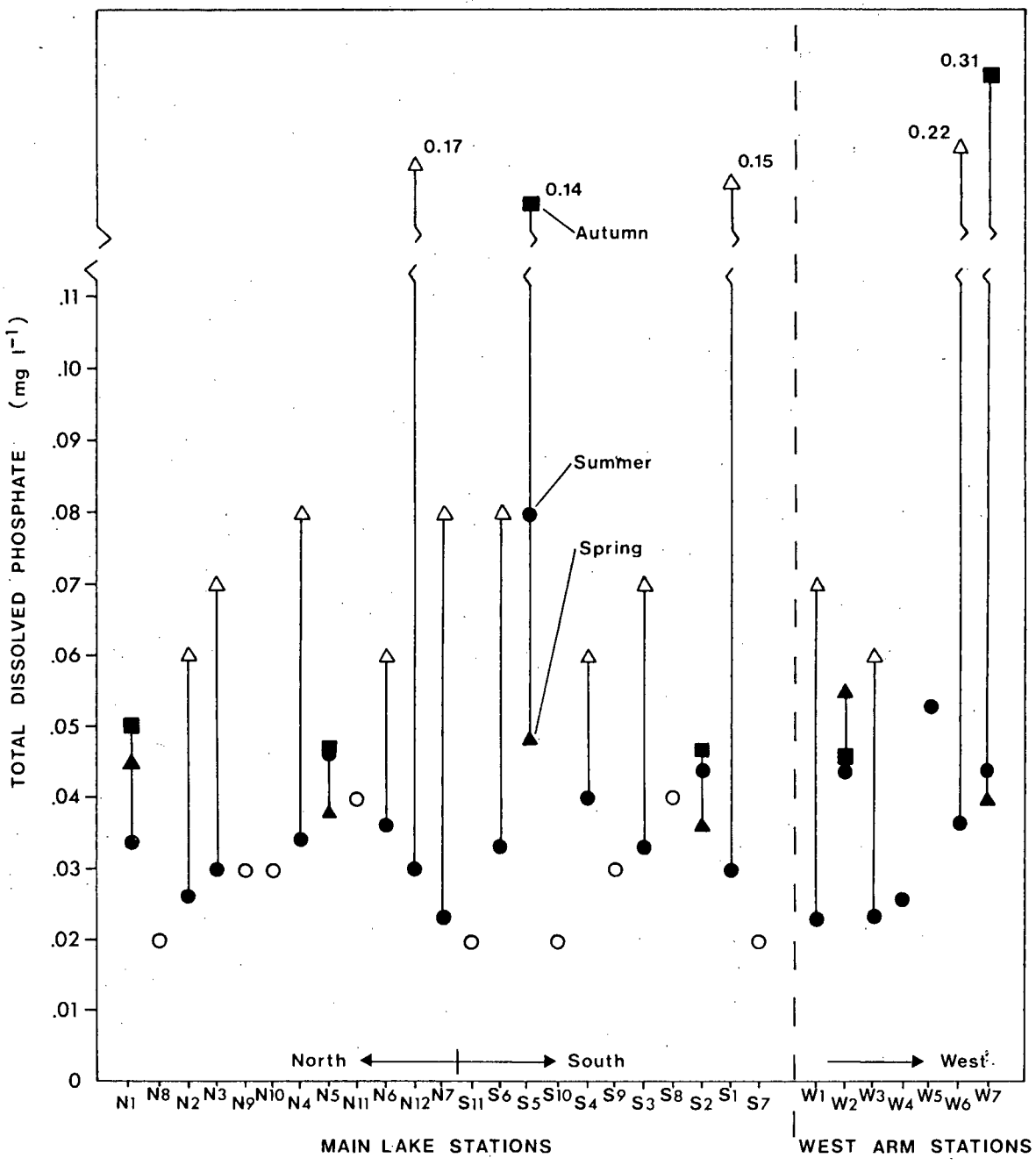


Fig. 14. Regional variations in total dissolved phosphate (as P) content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

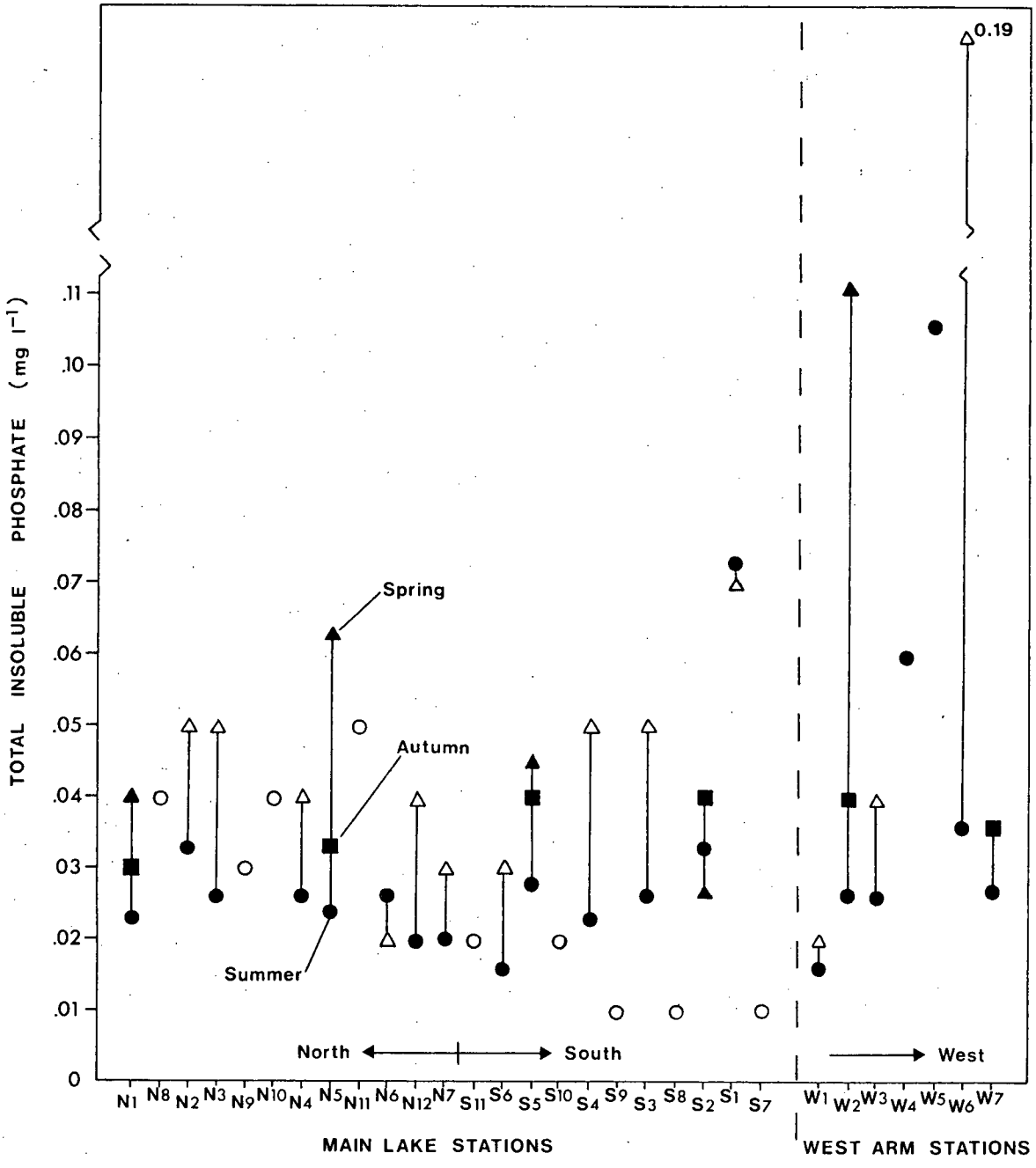


Fig. 15. Regional variations in total insoluble phosphate (as P) content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

(as indicated by the open circles and open triangles in the figures) there is no apparent phosphate gradient. Lack of phosphate gradient could attest to its biological utilization rather than within lake homogeneity of phosphorus. If the phosphate was utilized only by planktonic algae, total phosphate readings, which include an analysis of cellular phosphorus, might show the expected within lake pattern. In Kootenay Lake's inshore waters, total phosphate does not show a gradient probably because of phosphorus utilization and storage by attached algae, which are not present in chemical water samples (see section on attached algal phosphorus storage).

Dissolved orthophosphate nutrient levels are highest in the spring and lowest during the summer (Fig. 13). Nutrient levels are exceptionally high in early May at the start of freshet (open triangles in the figures) and decrease in later spring. Samples collected in early July (open circles) were the lowest in phosphorus with most concentrations being 0.02 mg l^{-1} or less. The summer decrease in phosphorus is apparently common in all lakes. It is often attributed to biological utilization. Loadings (calculated by multiplying river concentrations by discharge) of phosphorus and other chemical ions are also less during the summer, since less water enters the lake then than during spring freshet. Because of the summer decrease in phosphorus, Vollenweider (1971), Dillon and Rigler (1974), Edmondson (1972) and others use late winter or spring maximum phosphorus values in determining a lake's trophic state and predicting the planktonic algal biomass for the next summer. The occurrence of a blue-green algal bloom during summer 1973 on Kootenay Lake was not unexpected, considering its high (> 0.05 mg l^{-1}) spring orthophosphate concentrations.

Phosphate concentrations in the west arm of the lake show the same seasonal trends as in the main lake. Levels are comparable to the main lake and increase towards the lake outlet, although the trend is not consistent. Loading data in this region of the lake has shown very high levels (Northcote, 1972b, 1973a), which cannot be attributed to the phosphate fertilizer plant operations alone.

Dissolved orthophosphate varies with depth (Table I). Water from 0.1 m depth had the lowest concentrations (0.02-0.025 mg l^{-1} averages). Despite the vast differences in loadings to the north and south arms of the lake, a phosphorus gradient did not occur within the lake. Water from the 3.0 m depth had the highest amounts (0.02-0.07 mg l^{-1} averages) of orthophosphate. While there was not a definite phosphate gradient at the 3.0 m depth, the south arm of the lake did have the highest levels.

Total dissolved phosphorus and total insoluble phosphorus showed trends that were similar to those for dissolved orthophosphate (Fig. 13, 14, 15). There were no nutrient gradients within the lake, and spring values were higher than summer values. Levels of total dissolved phosphorus are generally 0.03-0.04 mg l^{-1}, only 25% higher than dissolved orthophosphate levels. Total insoluble phosphorus had a concentration of around 0.03 mg l^{-1} and was not as variable as the other phosphate species.

Nitrogen

The main inorganic nitrogen forms found in water are dissolved nitrogen gas, ammonia, nitrate and nitrite salts (McCarty, 1970). In well oxygenated lakes such as Kootenay, nitrate - nitrogen is dominant and the

Table I. Mean dissolved orthophosphate (as P) content of inshore Kootenay Lake water at the 0.1, 1.0, 3.0, and 5.0 m depths.

Depth	Station					
	N1	N5	S5	S2	W2	W7
0.1 m	.025	.023	.023	.020	.023	.023
1.0 m	.027	.030	.030	.028	.027	.027
3.0 m	.020	.028	.073	.035	.020	.038
5.0 m	-	.025	.037	.020	.020	.030

only form likely to be utilized by autotrophs (Keeney, 1972; Lee, 1970; McCarty, 1970).

Nitrate - nitrogen concentrations in Kootenay Lake's 1.0 m mid-lake water ranged from 0.02-0.09 mg l^{-1} with no apparent within lake gradient (B.C. Pollution Control Branch, unpublished data; Fig. 16). Inshore nitrate values obtained during this study are not presented, as laboratory problems invalidated the results. However, there is probably little difference between inshore and mid-lake nitrate readings. Inshore nitrate samples collected during 1971 (Water Quality Branch, 1974) had levels of about 0.05 mg l^{-1} which are comparable to mid-lake concentrations. Nitrate concentrations have shown little change from 1949 to the present, which is not surprising since nitrate loadings to the lake have shown little change (Northcote, 1973a).

Total Dissolved Solids

Total dissolved solids (TDS) content of Kootenay Lake 1.0 m inshore water usually ranges from 50-80 mg l^{-1}, with some values near spring freshet being over 100 mg l^{-1} (Fig. 17). These data tend to be lower than concentrations of 80-100 mg l^{-1} reported by Northcote (1973a). Kootenay Lake's TDS levels are typical of British Columbia waters, levels of 100 mg l^{-1} being close to the average obtained from a study of 100 B.C. lakes (Northcote and Larkin, 1956).

Regionally, there are more total dissolved solids in the south end of the lake, concentrations decreasing northward except for a slight increase at station N1 near the Duncan River inlet. West arm TDS concentrations are similar to south arm concentrations.

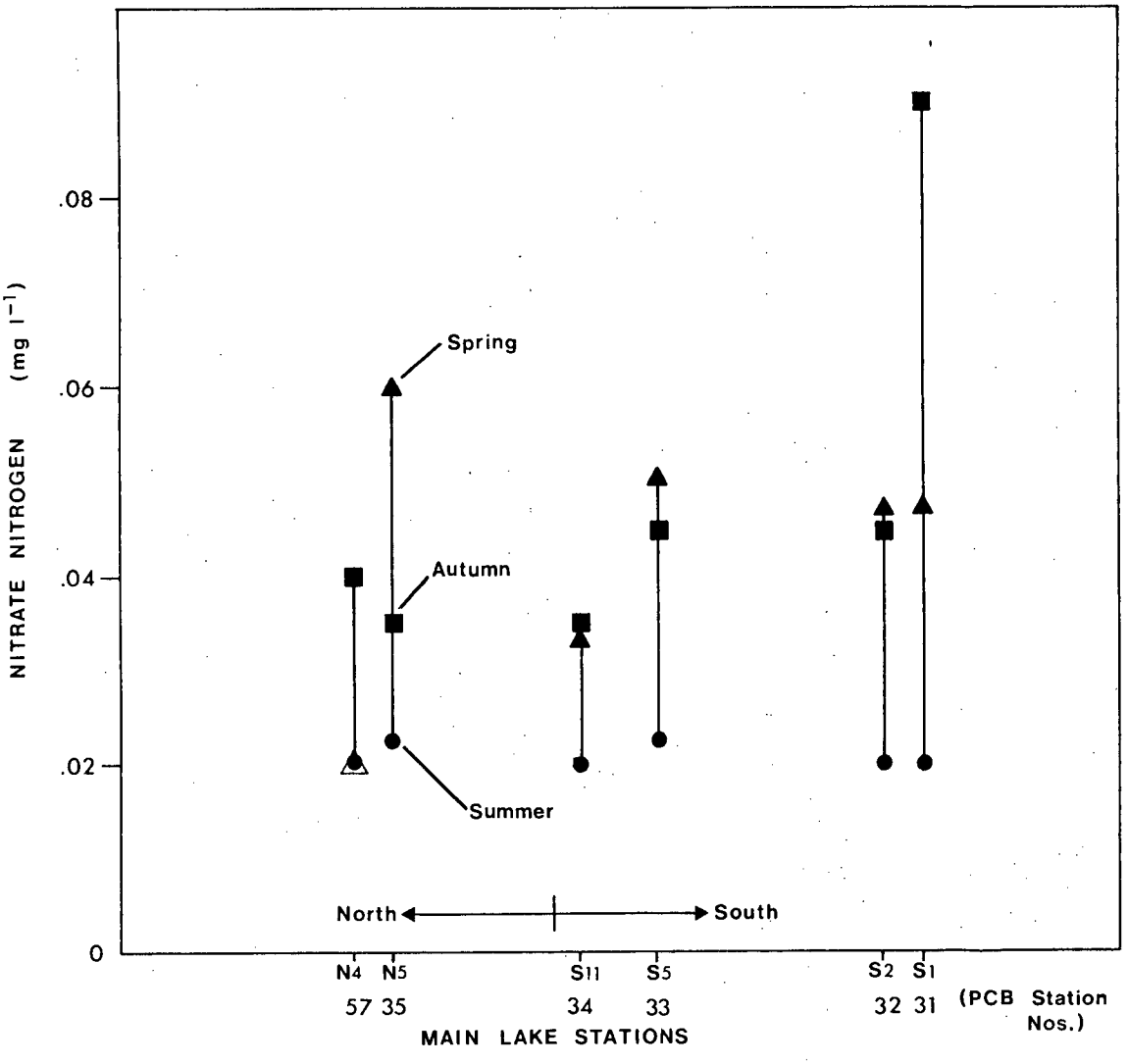


Fig. 16. Regional variations in dissolved nitrate nitrogen content of 1.0 m deep midlake Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open triangle represents a single measurement in June. Drawn from data supplied by the B.C. Pollution Control Branch.

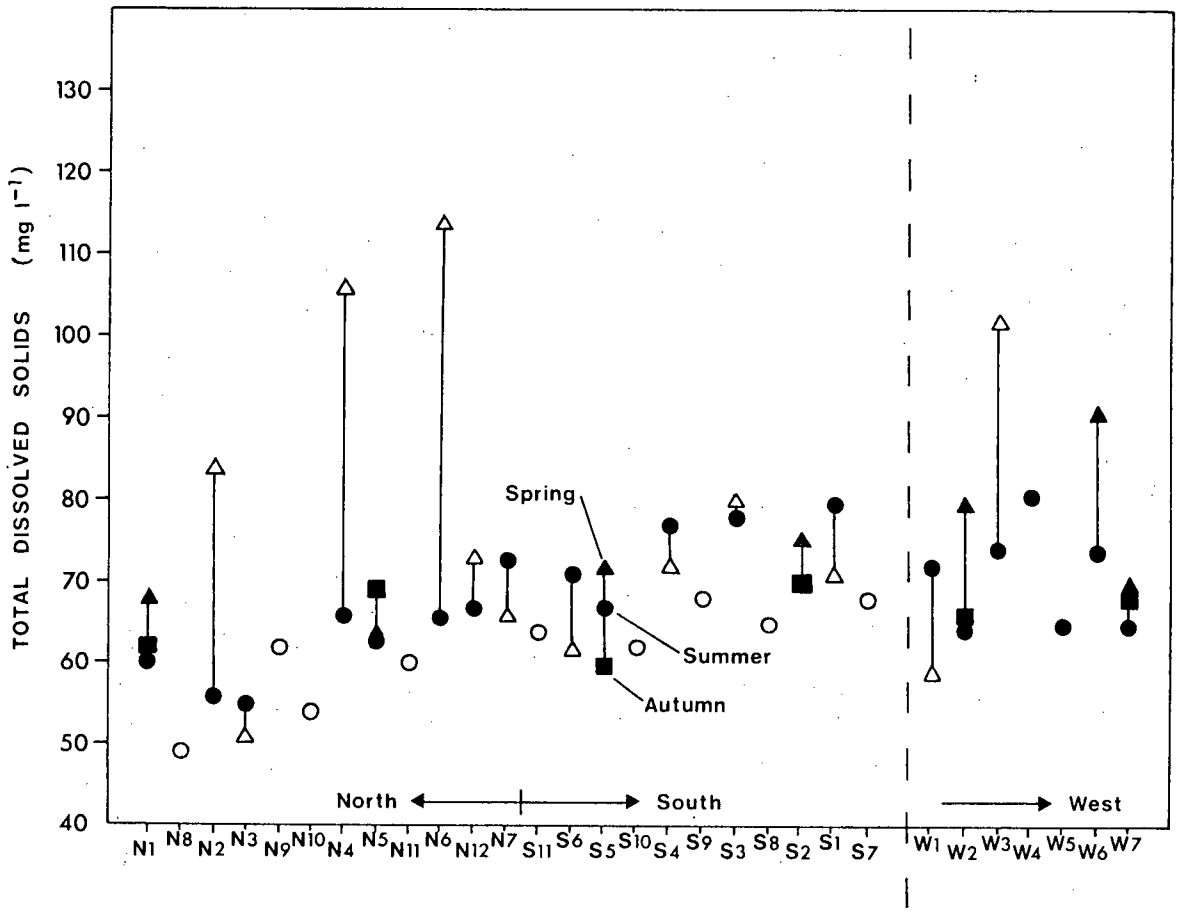


Fig. 17. Regional variations in total dissolved solid content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

Alkalinity and pH

Carbon is plentiful in Kootenay Lake with total carbon (all in the form of CO_2 and HCO_3^-) concentrations of between 45-65 mg l^{-1} (Fig. 18). Highest alkalinity concentrations (often > 60 mg l^{-1}) occur in Kootenay Lake during spring freshet; lowest concentrations (often < 50 mg l^{-1}) occur during the summer (Fig. 18). Alkalinity, according to mean summer values, is highest in the south end of the lake (generally > 50 mg l^{-1}) and decreases northwards (generally < 50 mg l^{-1}) (Fig. 18). Transport of carbon ions by the Kootenay River into the south end of the lake probably creates the gradient. Alkalinity levels in the Kootenay River just before it enters Kootenay Lake are higher than the lake levels (Northcote, 1973a).

Carbon compounds are intricately connected in pH related equilibria. Decreases in CO_2 caused by algal utilization result in HCO_3^- shifts to CO_2 and subsequent decreases in hydrogen ions result in pH increases. The gradual reduction in Kootenay Lake's alkalinity over the years (Northcote, 1973a) and the corresponding increase in pH are probably caused by denser algal populations. pH values of between 7.5 and 8.0 that I recorded (Fig. 19) are lower than 1960 levels, and are more characteristic of early 1950 conditions. This trend perhaps indicates that algal populations, in response to slightly lower phosphate concentrations, are no longer increasing.

Silica

Concentrations of silica in 1.0 m Kootenay Lake water range from 1.0 to 7.0 mg l^{-1} (Fig. 20) and are comparable to a 1961 value of 2.0 mg l^{-1} (Engineering Division Health Branch, MS 1965). During this study, levels were highest in the spring freshet period and lowest in the summer, after loadings decreased and after diatom cells utilized much of the silica (Fig. 20).

FIGURE 18

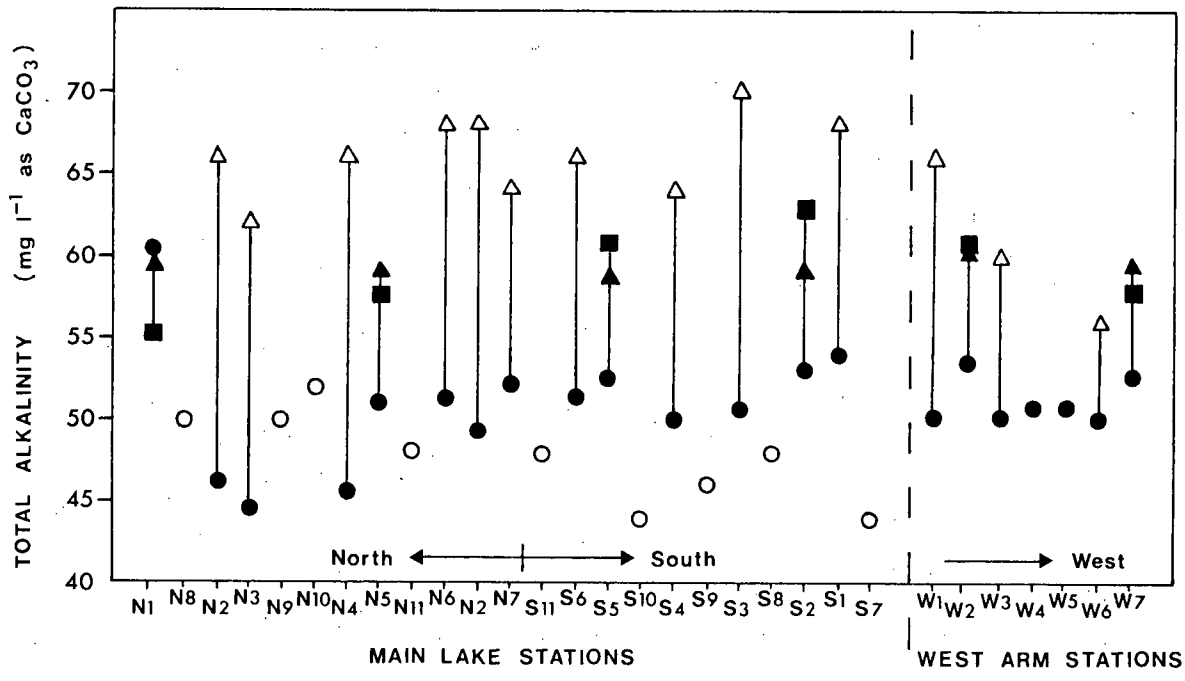


Fig. 18. Regional variations in total alkalinity of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

FIGURE 19

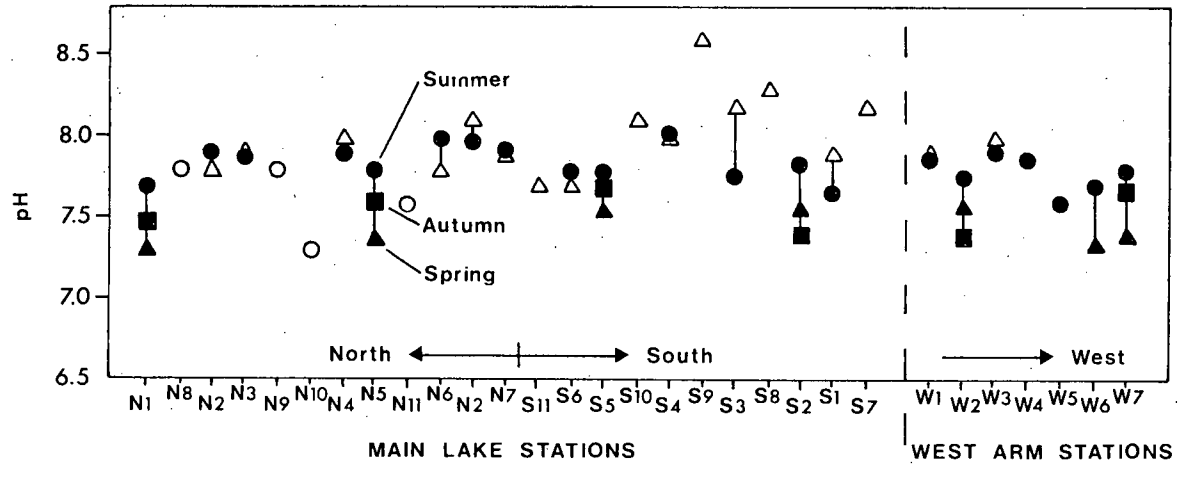


Fig. 19. Regional variations in pH of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

Concentrations did not drop below 1.0 mg l^{-1}, which is well above the critical level of 0.1 mg SiO_2 l^{-1} which Schelske and Stoermer (1971) claim to be silica's limiting concentration. A study of the lake's sediments indicates that large amounts of quartz (silica) particles are washed into the lake from the Kootenay River inlet, which would compensate for diatom depletions (Ennis, Northcote, and Stockner; unpublished). Silica concentrations are slightly higher in the south arm of the lake (> 2.5 to 7.0 mg l^{-1}) than in the north and west arms (1.0 to 5.4 mg l^{-1}) (Fig. 20).

Calcium

Calcium concentrations in Kootenay Lake are above 16 mg l^{-1}, and are unlikely to affect algal growth since calcium is needed in only trace amounts. Spring and average summer concentrations in the lake show a pronounced gradient with higher levels at the south end of the lake (Fig. 21). The cation can be reduced with photosynthesis though, through chemical precipitation. A reduction in HCO_3^- alkalinity by algal incorporation causes an increase in pH which decreases the solubility of Ca and there is $CaCO_3$ precipitation (Ruttner, 1963). This could explain the July calcium minimum and reverse north-south gradient, since higher phosphate inputs to the south end of the lake allow greater algal populations to exist there, and more precipitation of calcium to occur. Shortly after the July calcium minimum a planktonic blue-green *(Anabaena)* algal bloom became noticeable at the south end of the lake.

Sodium

Sodium is the most abundant member of the alkali-metal group

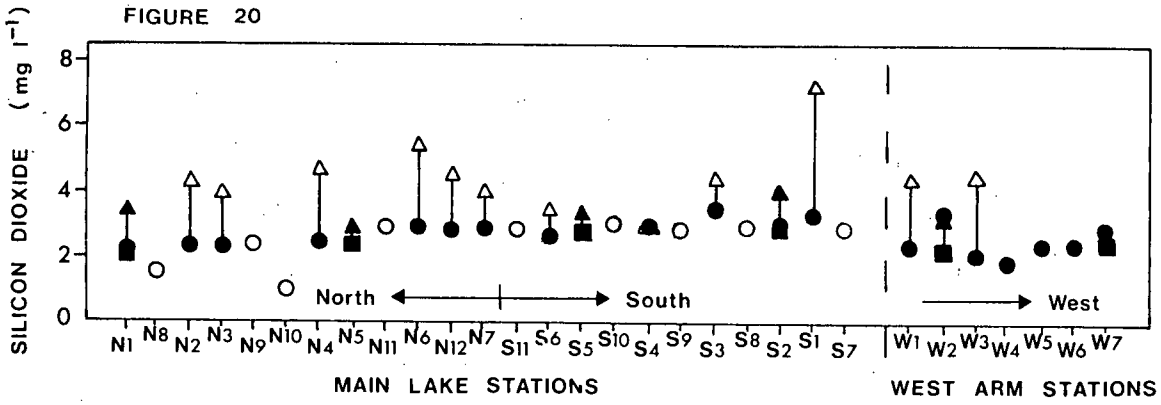


Fig. 20. Regional variation in silica (SiO_2) content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

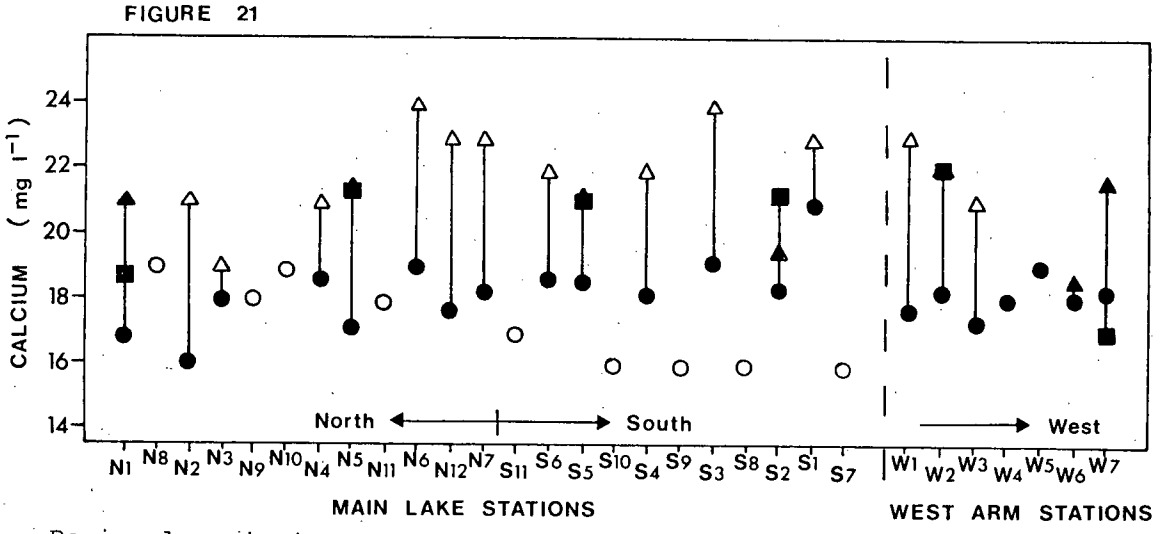


Fig. 21. Regional variations in calcium content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

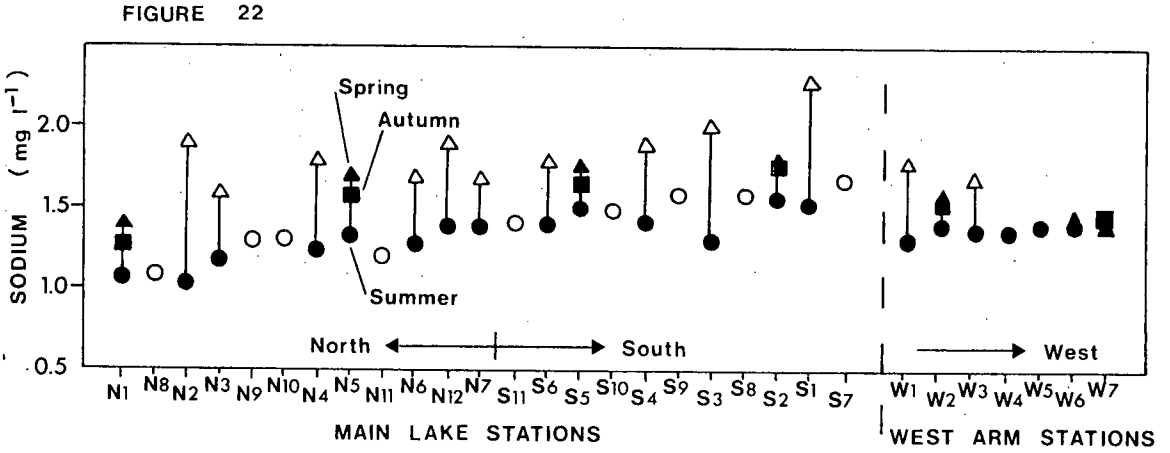


Fig. 22. Regional variations in sodium content of 1.0 m deep inshore Kootenay Lake water, 1973. Solid symbols represent seasonal averages, open symbols represent single measurements.

(Hem, 1970), but is needed in only small amounts for algal growth. Concentrations in Kootenay Lake are generally under 2.0 mg l^{-1}. There is a distinct gradient in the lake with highest values (2.3 mg l^{-1}) at the south end, and lowest values (1.0 mg l^{-1}) at the north end (Fig. 22).

ATTACHED ALGAE

Abundance

1. Chlorophyll a

Highest chlorophyll a values recorded in this study (readings up to 63 µg cm $^{-2}$) occurred at the 0.1 m depth, during periods of stable water levels (Fig. 5) in early May. (Biological data for all samples collected are stored on computer tape, available from the Institute of Animal Resource Ecology, Biological Data Centre at the University of British Columbia.) However, water levels usually fluctuated throughout the summer and chlorophyll a content near the lake surface was less, on the average, than at other depths. (Fig. 23, 24). Chlorophyll a content was also low at the 1.0 m depth (Fig. 23) with values near 3 µg cm $^{-2}$ in the south arm and lower values elsewhere. Data from the 3.0 m depth (Fig. 23) also indicate that attached algal populations are densest in the south arm, with average chlorophyll a readings of about 8 µg cm $^{-2}$ of rock surface. At this depth, chlorophyll gradually decreases to about 3 µg cm $^{-2}$ at the upper end of the north arm and to about 2 µg cm $^{-2}$ at station W7 at the lower end of the west arm. Station S6 located in Crawford Bay, isolated from the main lake, has an unusually high chlorophyll content of about 17 µg cm $^{-2}$. Amounts and distribution of chlorophyll at the 5.0 m depth (Fig. 23) are similar to patterns recorded at the 3.0 m depth. Both the 3.0 and 5.0 m depths also had their highest chlorophyll a content during summer (Fig. 24), in contrast to the spring maximums at the 0.1 and 1.0 m depths.

2. Organic Weight

Organic weight estimates of community biomass differed somewhat from

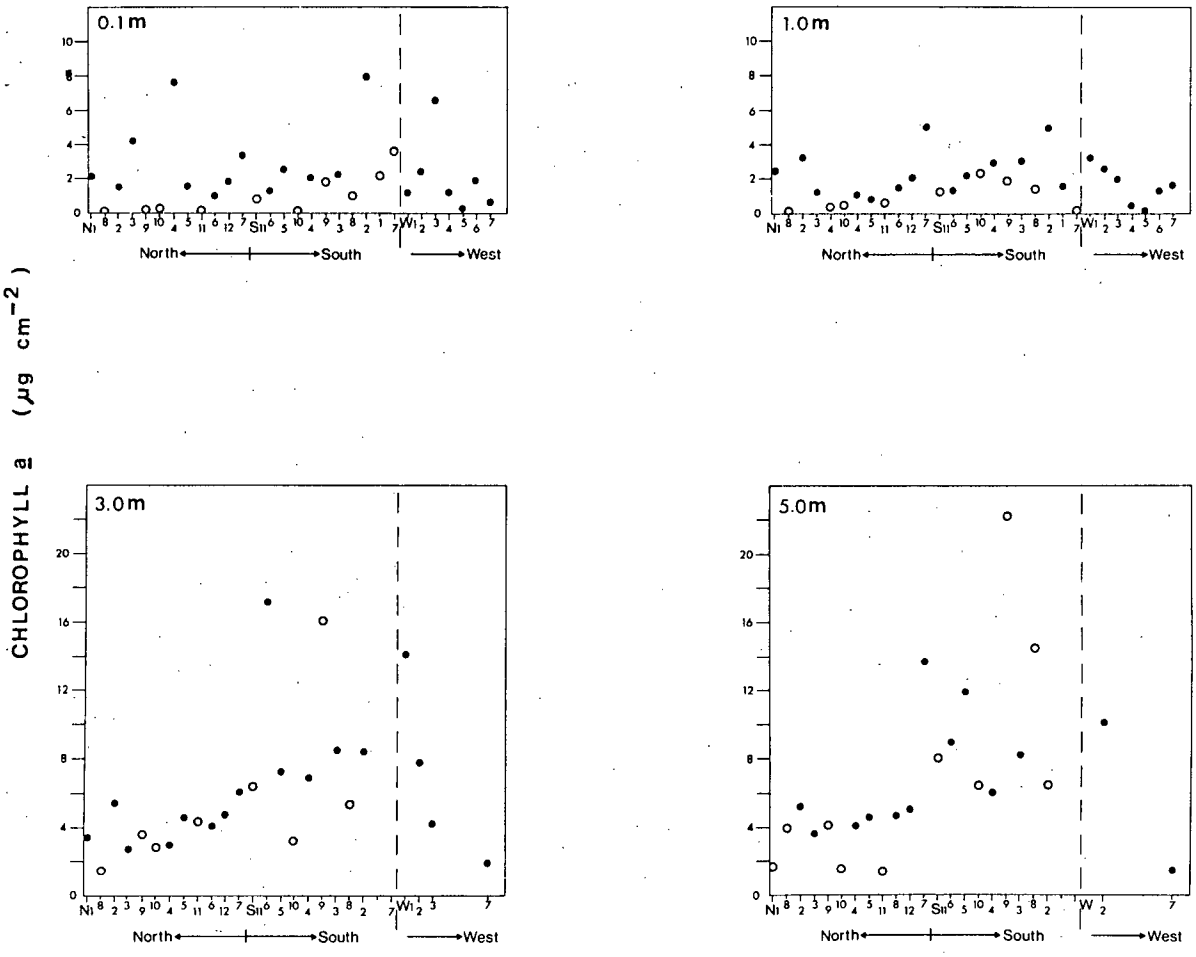


Fig. 23. Regional variations in yearly average chlorophyll a concentrations at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Solid circles represent yearly averages, open circles represent single measurements in early July.

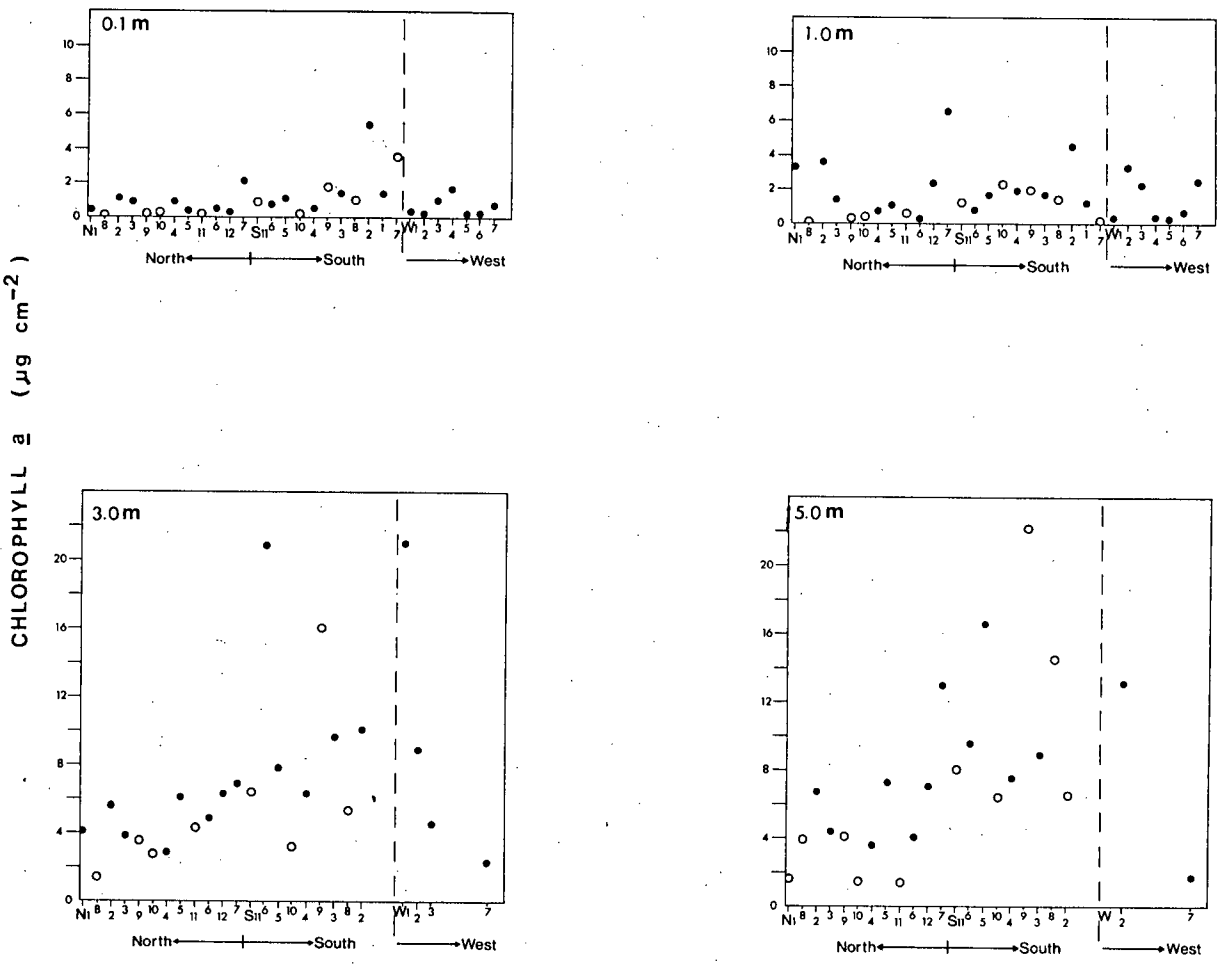


Fig. 24. Regional variations in average summer chlorophyll a concentration at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Solid circles represent summer averages, open circles represent single measurements in early July.

chlorophyll a estimates (Fig. 25). Whereas chlorophyll a content increased towards the south end of the lake, organic weights were similar (some depths had slightly more organics in the south arm) throughout the main lake. This difference is surprising, as a regression of organic weight versus chlorophyll a showed the two estimates of biomass to be highly correlated (Fig. 26). But at low biomasses the relationship between organic weight and chlorophyll a exhibits much scatter (Fig. 26), which may partially explain the different trends in the two parameters. Moreover, the sampling schedule probably accounts for most of the differences. Three of the five chlorophyll sampling periods were during summer, when phosphorus levels were low and therefore likely to limit the algal populations. The higher chlorophyll abundances in the south arm (where phosphorus loading is highest) are therefore not unexpected. Organic weights were sampled up to twenty times during the study, on several occasions during high phosphorus conditions when that nutrient was less likely to limit algal abundance. An organic weight gradient (using yearly averages) would therefore be less likely than a chlorophyll gradient. However, during early July when phosphorus concentrations were low, organic weights were consistently greater (paralleling chlorophyll a results) in the south arm of the lake than in the north arm (Fig. 27).

Yearly mean data (Fig. 27) did show both the 1.0 and 5.0 m depths to have slightly more organic weight determined biomass in the south arm of Kootenay Lake than in the north arm. There was no obvious yearly regional variation at the 0.1 and 3.0 m depths.

The vertical distribution of biomass determined by organic weight was similar to the chlorophyll a pattern, with the shallower 0.1 and 1.0 m

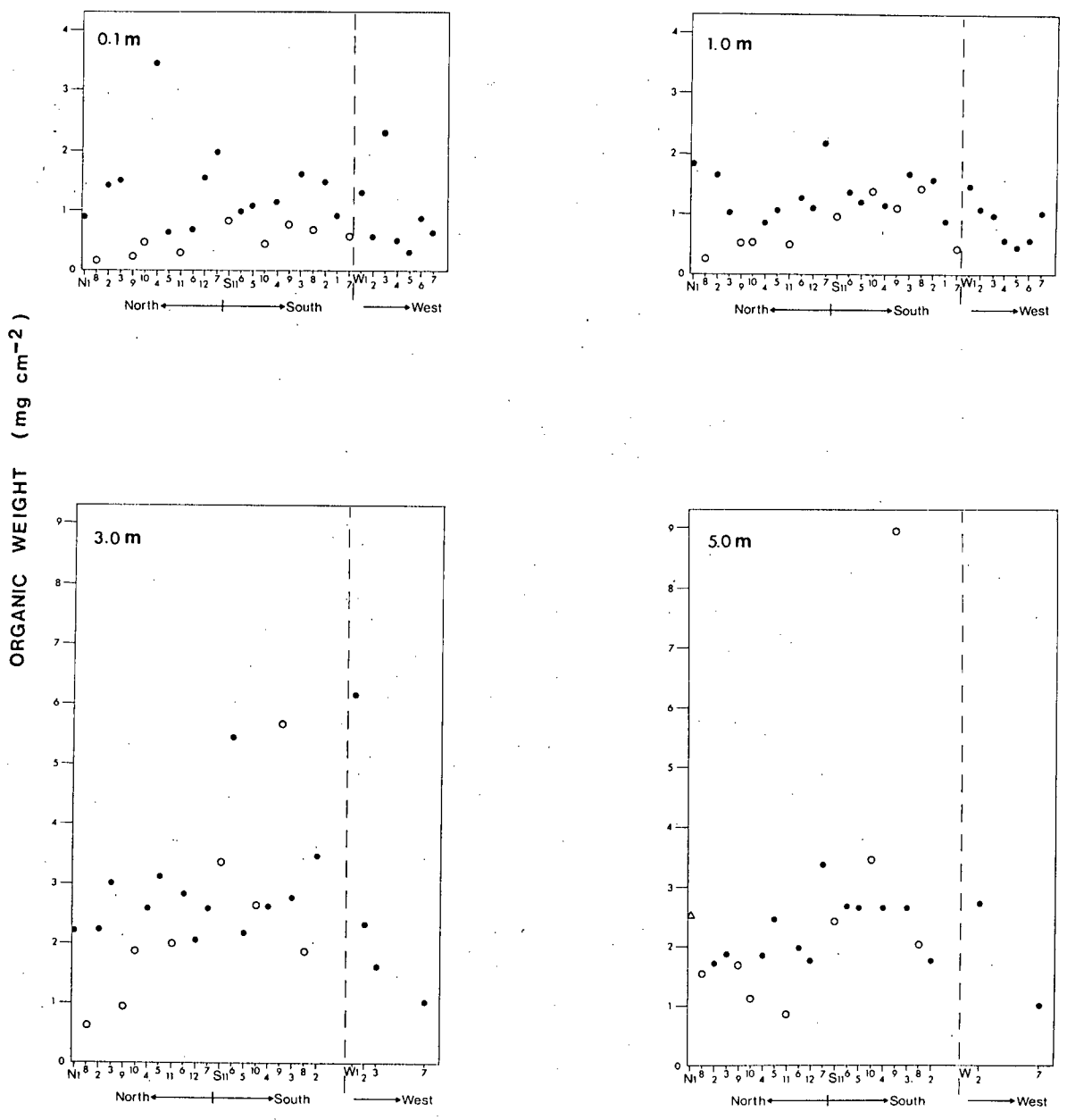


Fig. 25. Regional variations in yearly average organic weight levels at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Solid circles represent yearly averages, open symbols represent single measurements.

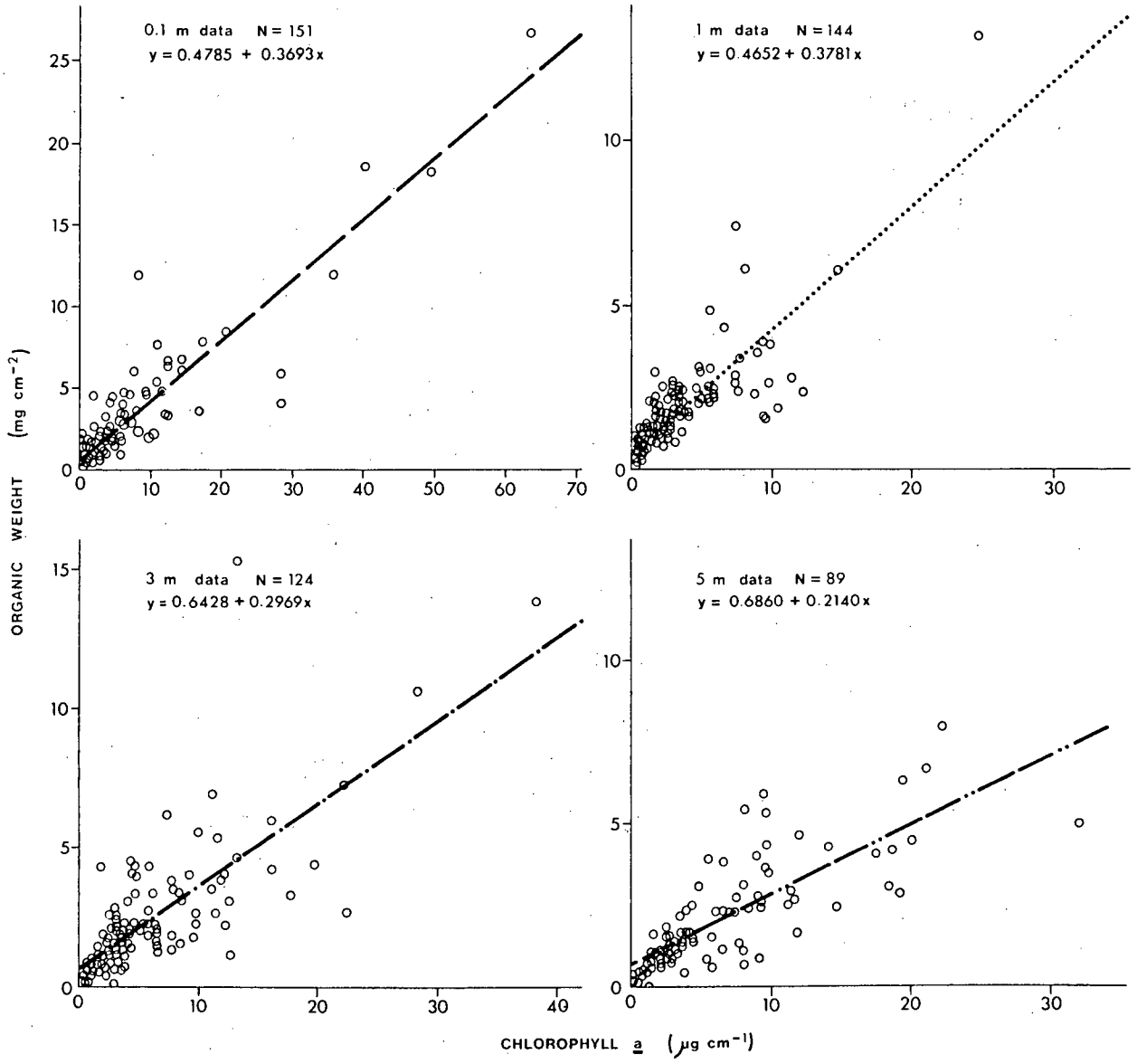


Fig. 26. Relationship between organic weights and chlorophyll a for 510 attached algal samples at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973.

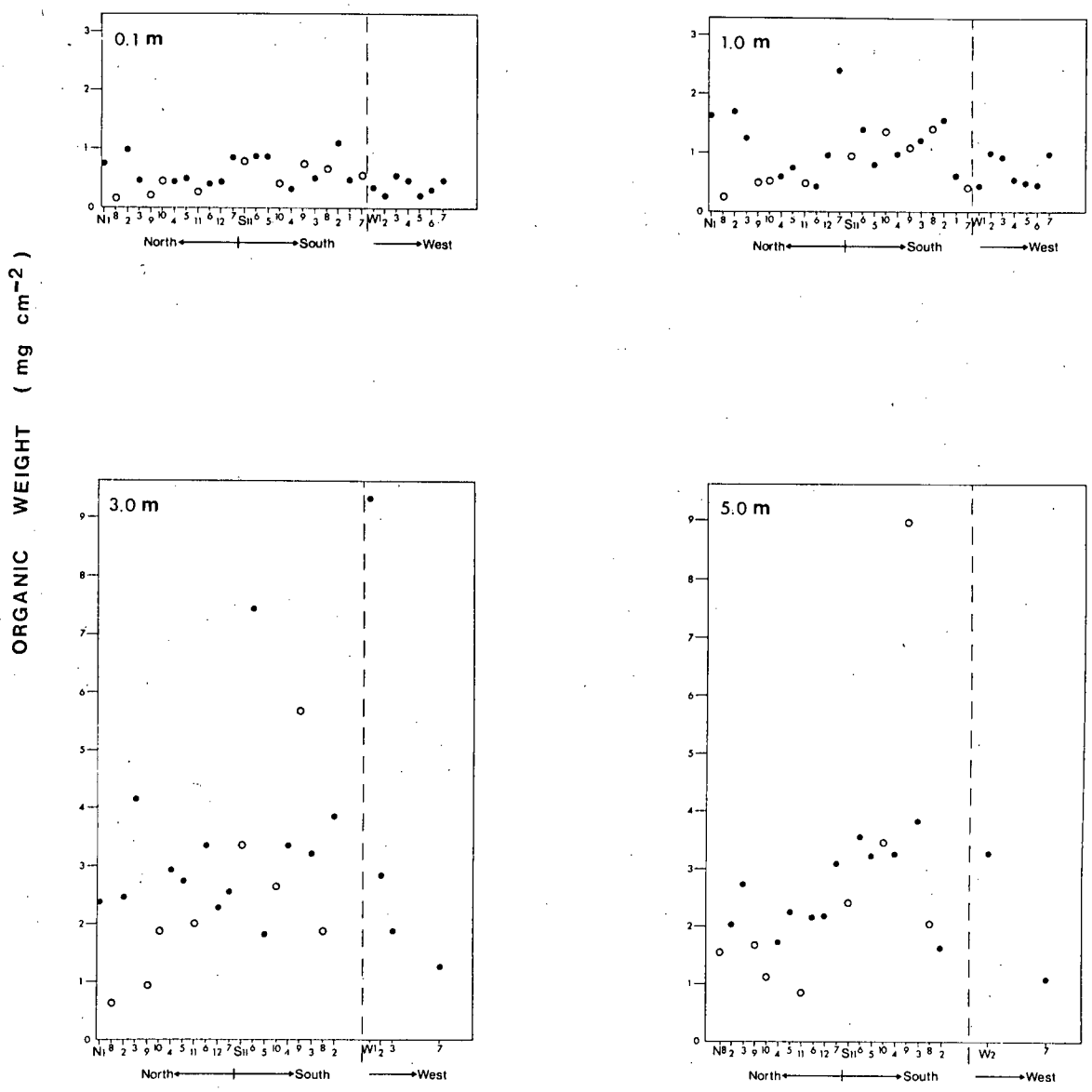


Fig. 27. Regional variations in average summer organic weight levels at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Solid circles represent summer averages, open circles represent single measurements in early July.

depths having less biomass (generally < 2 mg cm $^{-2}$) than the 3.0 and 5.0 m depths (generally > 2 mg cm $^{-2}$; Fig. 25). Data from a single sampling period in early September (Fig. 28) clearly shows the vertical distribution of both chlorophyll a and organic weight determined biomass. In both the north and south arm stations, biomass increases to the 5.0 m depth and then decreases. On a relative basis (note different scales in Fig. 28), organic weight indicated greater biomass than chlorophyll at the shallower depths, but the reverse was true at the deeper depths. More chlorophyll is probably needed at the lower depths to utilize the reduced light energy. Regressions utilizing data from 510 samples that were analyzed for both organic weight and chlorophyll a also showed that below the 1.0 m depth the amount of chlorophyll a increased relative to the organic weight (Fig. 26).

The seasonal variation of organic weights paralleled the chlorophyll a pattern. An early May biomass peak at 0.1 m produced the highest organic weight values in the study, with one sample having 26.5 mg organic cm $^{-2}$. Biomass at 0.1 m were very low during the rest of the year (Fig. 29), with a slight increase in August when fluctuations in water level were slight. Spring readings were also generally higher than summer readings at the 1.0 m depth (Fig. 27). As observed with the chlorophyll data, the deeper 3.0 and 5.0 m depths had higher values in summer than in spring. Winter values were close to the yearly means, except at the 1.0 m depth where organic weights were very high, especially in the north arm of Kootenay Lake.

Phosphorus Storage

Water extractable (surplus) phosphorus storage in algae ranged from about 0.15-2.50 µg P mg $^{-1}$ dry weight (Fig. 30, A). Lowest amounts

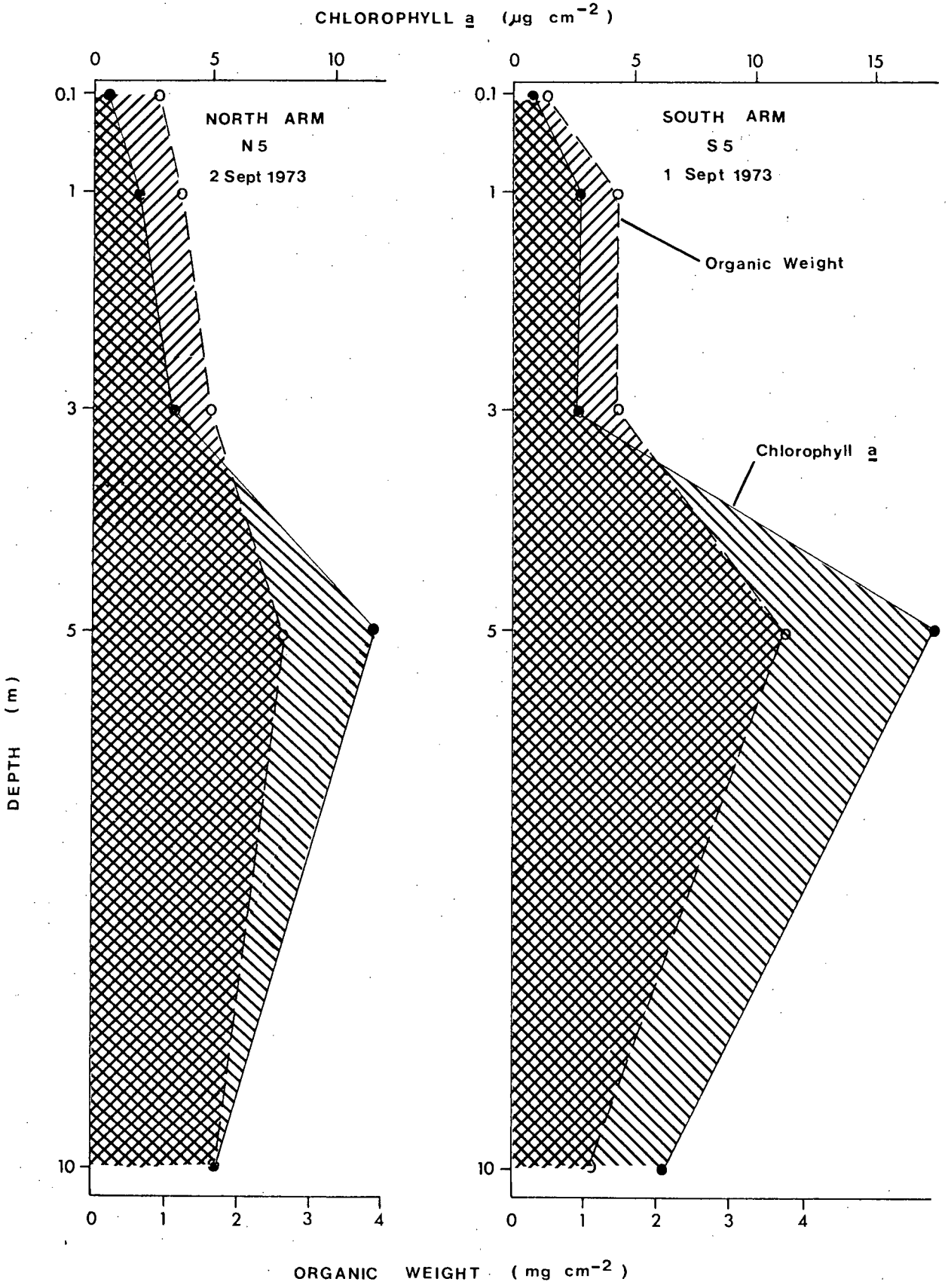


Fig. 28. Vertical variations in the amount of chlorophyll a and organic weight at a north arm (N5) and a south arm (S5) station in Kootenay Lake; 1, 2 Sept. 1973.

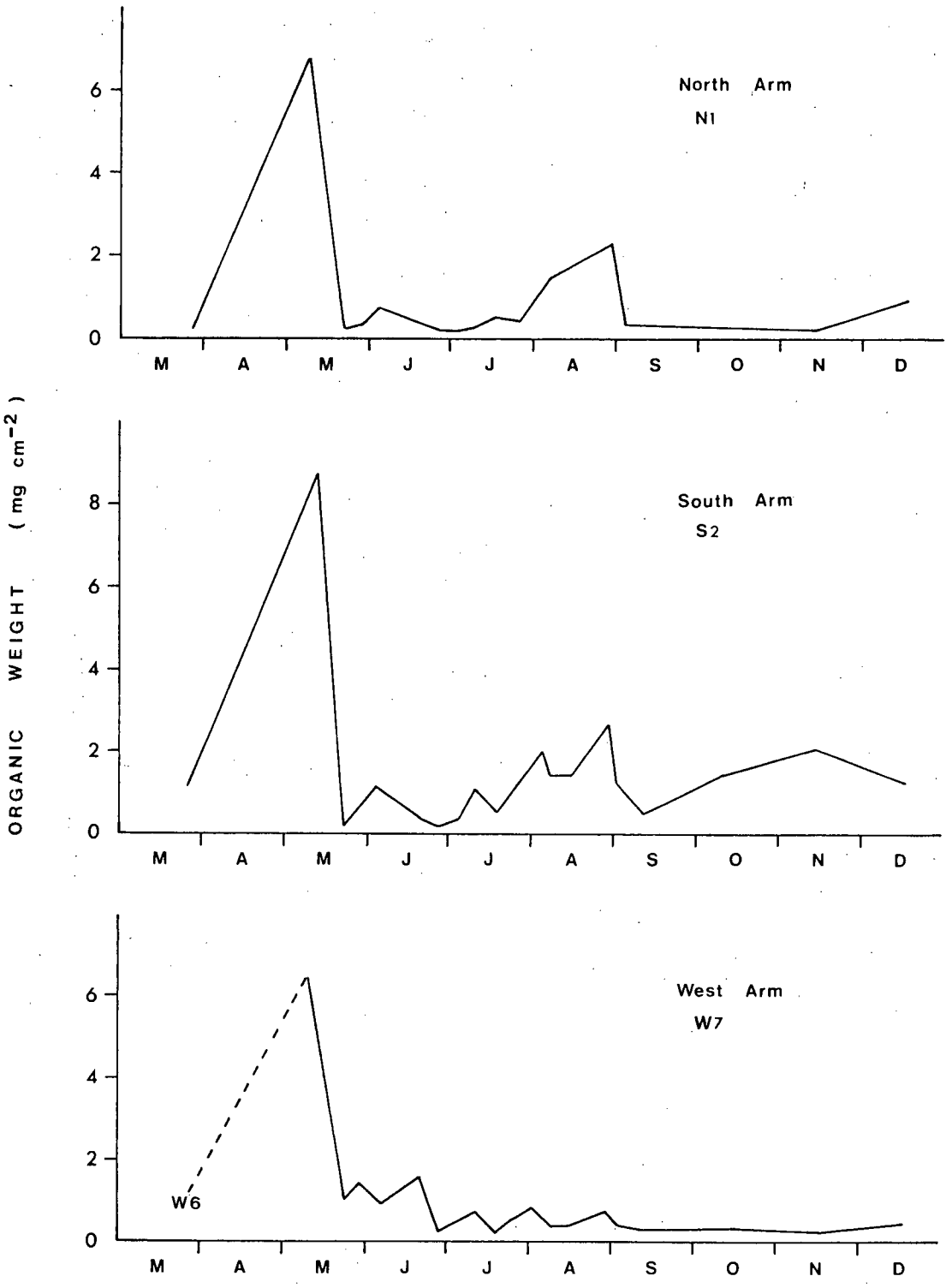


Fig. 29. Seasonal variations in the organic weight content of attached algae at 0.1 m in a north (N1), a south (S2), and a west (W7) arm station in Kootenay Lake, 1973.

of stored phosphorus, with some values below 1.0 μg mg $^{-1}$, occurred only in samples from north arm stations and in the westernmost station. Higher levels, indicating more eutrophic conditions (Lin, 1971), occurred in the south arm of the lake where readings were always above 1.0 μg mg $^{-1}$ dry weight algae. The surplus phosphorus gradient is not unexpected since phosphate loadings to the south end of the lake are high while north end loadings are low (Fig. 12). Paradoxically, the water phosphate data (Fig. 13-15) do not show south arm stations to be higher in phosphate, perhaps because it is rapidly picked up and stored by attached algal populations.

In addition to ambient phosphorus levels, algal abundances could influence the surplus phosphorus results. Low biomass in one region, for instance, could increase the surplus phosphorus levels per unit algae since there would be less algae to utilize the phosphorus. Consideration of the amount of surplus phosphorus per unit area of rock surface (Fig. 30, B) indicates that algal abundances have not greatly affected the surplus phosphorus gradient, except that the 0.1 m depth of station S5 has a lowered concentration. Surplus phosphorus ranges from about 5-30 μg cm $^{-2}$ rock surface with highest values in the south arm and lower values in the north and west arms of Kootenay Lake.

Production

Attached algal production was measured every two weeks from early May until mid-September. Daily growth rates near the lake surface (0.1 m depth) ranged from about 0.001 to 0.05 mg organic cm $^{-2}$, with highest values in the south arm of the lake (Fig. 31), production decreasing both northwards and westwards. Contrary to the biomass results, highest production occurred

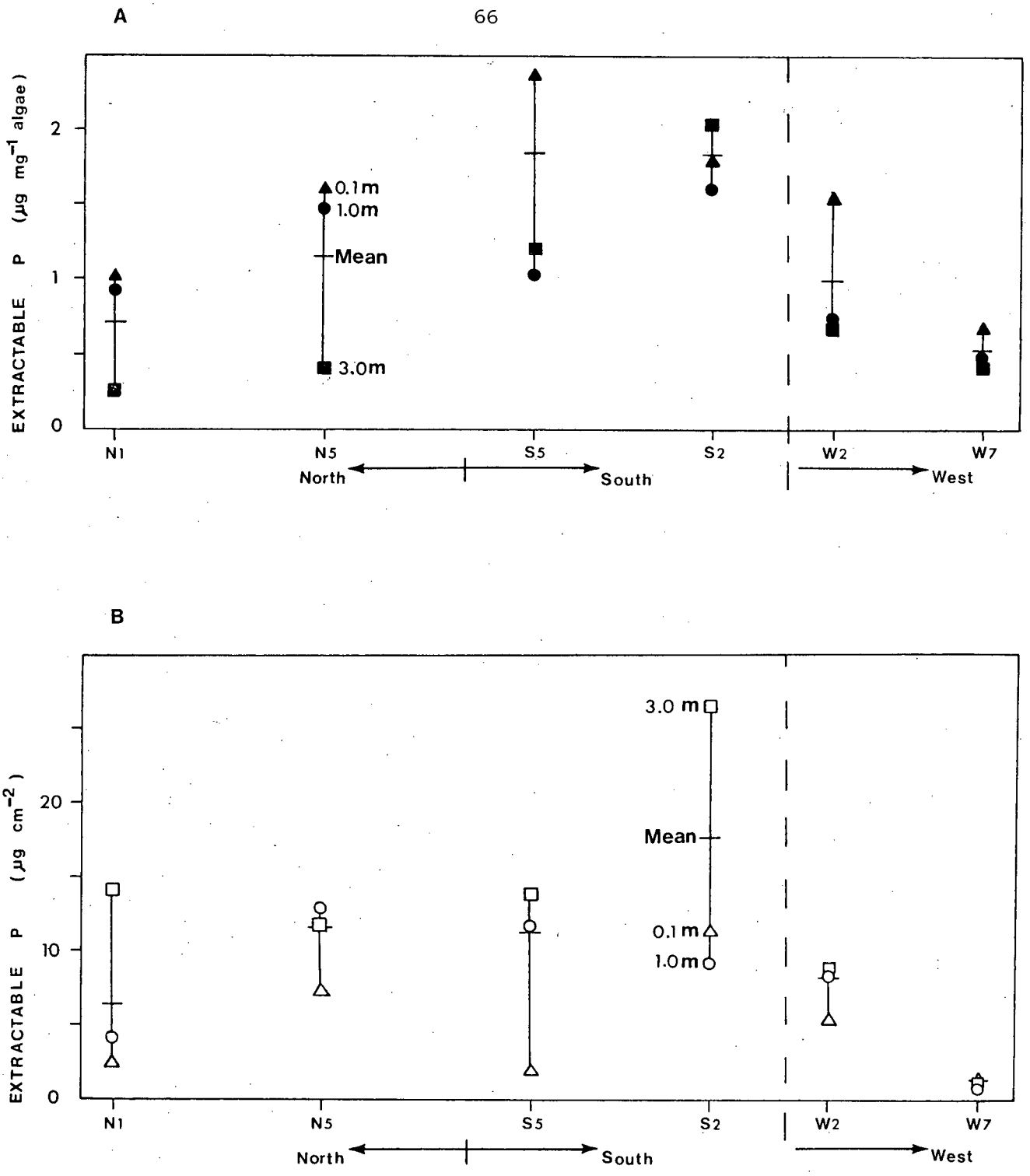


Fig. 30. A--Regional variations in the amount of boiling water extractable phosphorus per mg dry weight algae at 0.1, 1.0, and 3.0 m in Kootenay Lake, Nov.-Dec. 1973. B--Regional variations in the amount of boiling water extractable phosphorus per cm^2 rock surface at 0.1, 1.0, and 3.0 m in Kootenay Lake, Dec. 1973.

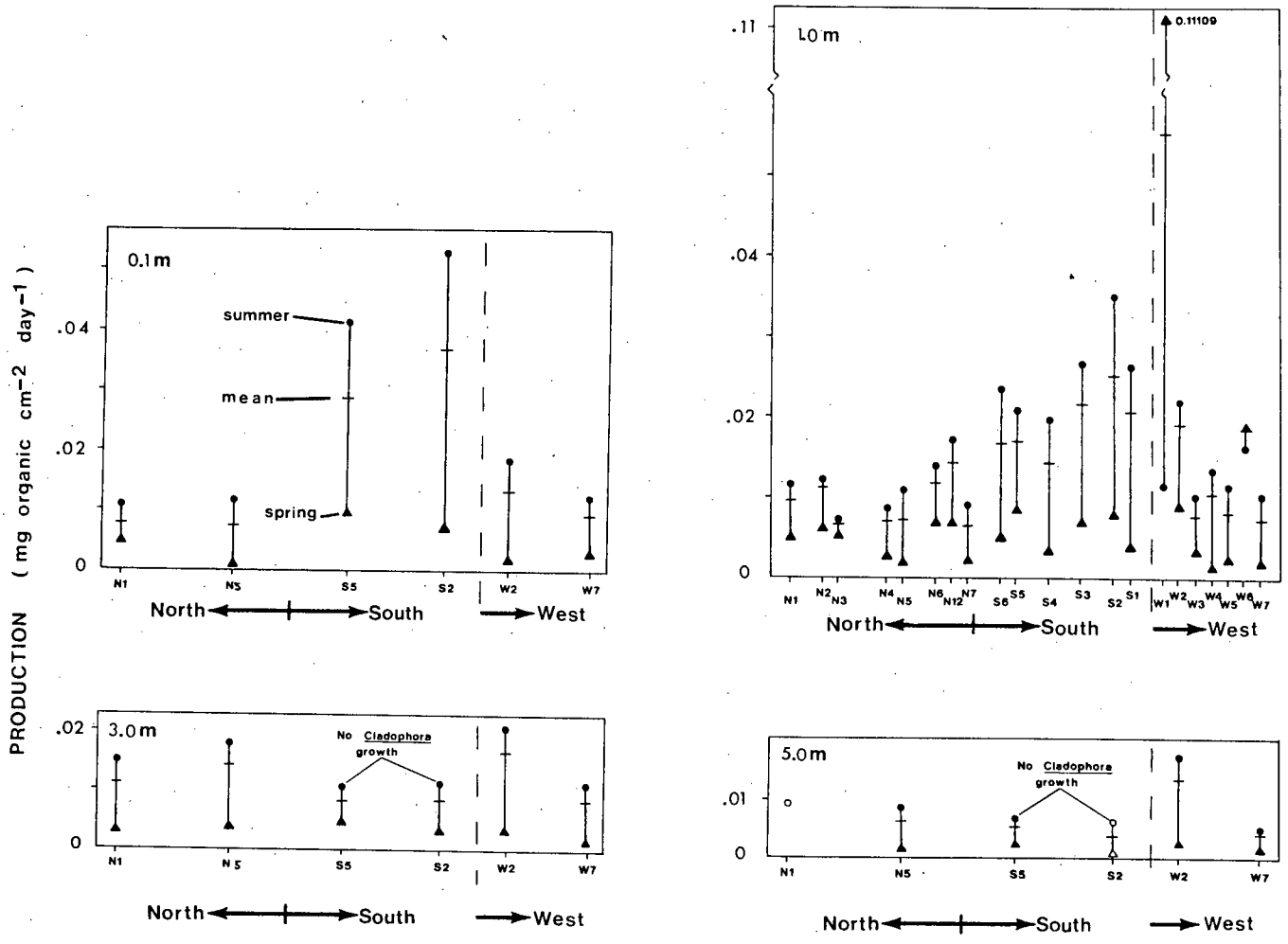


Fig. 31. Regional variations in average daily production (measured as mg organic cm^{-2}) of attached algae at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Horizontal bars represent yearly averages, solid symbols represent seasonal averages and open symbols represent single measurements.

in the summer rather than in the spring. This is probably an artifact of the sampling schedule, as the spring biomass peak occurred prior to measurements of growth rates.

Station W1, at the mouth of the west arm, was unique in having a spring growth peak one week later than at the other stations. Production at the 1.0 m depth there, from 8-23 May, 1973, was the highest recorded in this study (average daily growth rate of 0.32 mg organic cm $^{-2}$). At the 1.0 m depth, annual daily growth rates were generally about 0.02 mg organic cm $^{-2}$ in the productive south arm of the lake, decreasing to about 0.005 mg organic cm $^{-2}$ at the north and west extremities. Except for the 1.0 m depth at stations W1 and W6, growth rates were greater in the summer than in the spring at the 1.0, 3.0 and 5.0 m depths.

Regional variations in growth rates at the 3.0 and 5.0 m depths were minimal, with slightly greater production in the north arm than in the south arm. Average daily production values at the 3.0 and 5.0 m depths were approximately 0.01 and 0.005 mg organic cm $^{-2}$ respectively. Rates of growth were much lower than at the 0.1 and 1.0 m depths, which is surprising since biomasses were greater at the deeper depths. Reduced energy input may have resulted in slower growth at these depths. In the south arm production is undoubtedly underestimated, since the large green alga *Cladophora aegagropila* (L.) Rabh., a major component of the south arm algal community at the deep depths, did not grow on the plexiglas production substrates (see more detailed discussion below). If *Cladophora* could have grown on the artificial substrate, it seems likely that there would also have been a marked production gradient at the 3.0 and 5.0 m depths with highest values in the south arm of Kootenay Lake.

Community Composition

Diatoms (Chrysophyta-Bacillariophyceae) consistently dominated the attached algal flora of Kootenay Lake (Fig. 32). Green (Chlorophyta) and blue-green algae (Cyanophyta) were also present in most samples. In addition, three other algal groups (Pyrrhophyta, Cryptophyta, and Chrysophyta-Chrysophyceae) were occasionally present, but never contributed greatly to the algal biomass.

1. Natural Substrates

At the lake surface (0.1 m depth) the attached algal flora was composed mainly of diatoms (roughly 75-85 percent by volume) and green algae (10-20 percent) (Fig. 32). Blue-green algae made up about 5 percent of the algal biomass in the main part of the lake, increasing to approximately 20 percent in the populated west arm. Regional variation in the percent composition of the algal community was great but, except for the increase in blue-green algae along the west arm, there were no clear trends evident.

A similar situation prevailed at the 1.0 m depth except that diatoms were slightly (about 5 percent) more abundant and green algae less abundant than at the lake surface (Fig. 32).

At the 3.0 and 5.0 m depths, the algal community exhibited definite regional trends in the percentage abundancies of diatoms, green algae and blue-green algae (Fig. 32). At the south end of the lake about 80 percent of the attached algae consisted of diatoms. Diatom abundance steadily increased to over 90 percent at the north end of the lake. Green algae had an opposite gradient, forming less than 5 percent of the biomass at the north

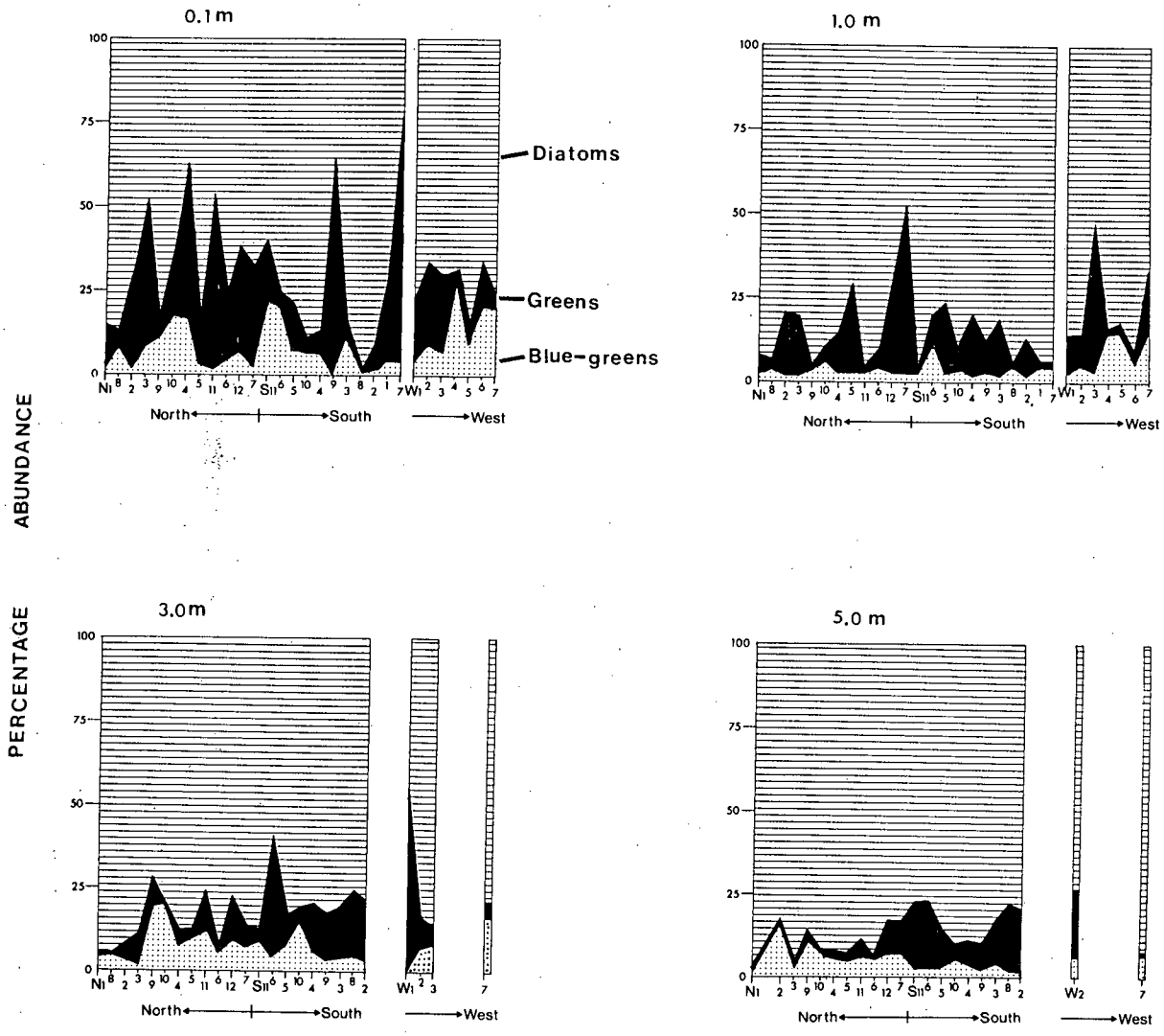


Fig. 32. Regional variations in average percentage abundance (by volume) of diatoms, green algae and blue-green algae attached to natural rock substrates at 0.1, 1.0, 3.0 and 5.0 m in Kootenay Lake, 1973.

end and about 20 percent of the biomass at the south end of Kootenay Lake. *Cladophora aegagropila* (L.) Rabh., which thrives in areas of high phosphorus content (Hoek, 1963), grew mainly in the south arm of Kootenay Lake and was primarily responsible for the increased green algal abundance (and decreased diatom percentage abundance) there. Blue-green algal trends were similar to those observed at the other depths, the main lake community consisting of about 5 percent blue-green algae, increasing to 10-20 percent along the west arm of the lake.

In the upper meter of Kootenay Lake there was a marked seasonal succession of the algal groups. While yearly averages (Fig. 32) showed the overall importance of the diatoms, there were periods in the year when green algae prevailed (Fig. 33). In early May at the 0.1 m depth, the spring growth peak consisted almost entirely of green algae (*Ulothrix* spp.), with diatoms predominating at other times. In contrast, at the 1.0 m depth there was a late summer-early fall growth peak of green algae (primarily *Spirogyra* sp.), diatoms being of major importance during spring and other sampling dates. Large changes in abundance of the algal groups did not occur at 3.0 and 5.0 m depths in the lake. There are indications though, that in the south arm green algae (primarily *Cladophora aegagropila*) were slightly more common in early fall than at other times. In the north arm of the lake, which had low phosphate loadings, *C. aegagropila* did not grow and green algae were never common (bottom graph of Fig. 33).

2. Artificial Substrates

The attached algal composition on artificial (production) substrates did not accurately reflect the composition on natural rock substrates (Fig. 34).

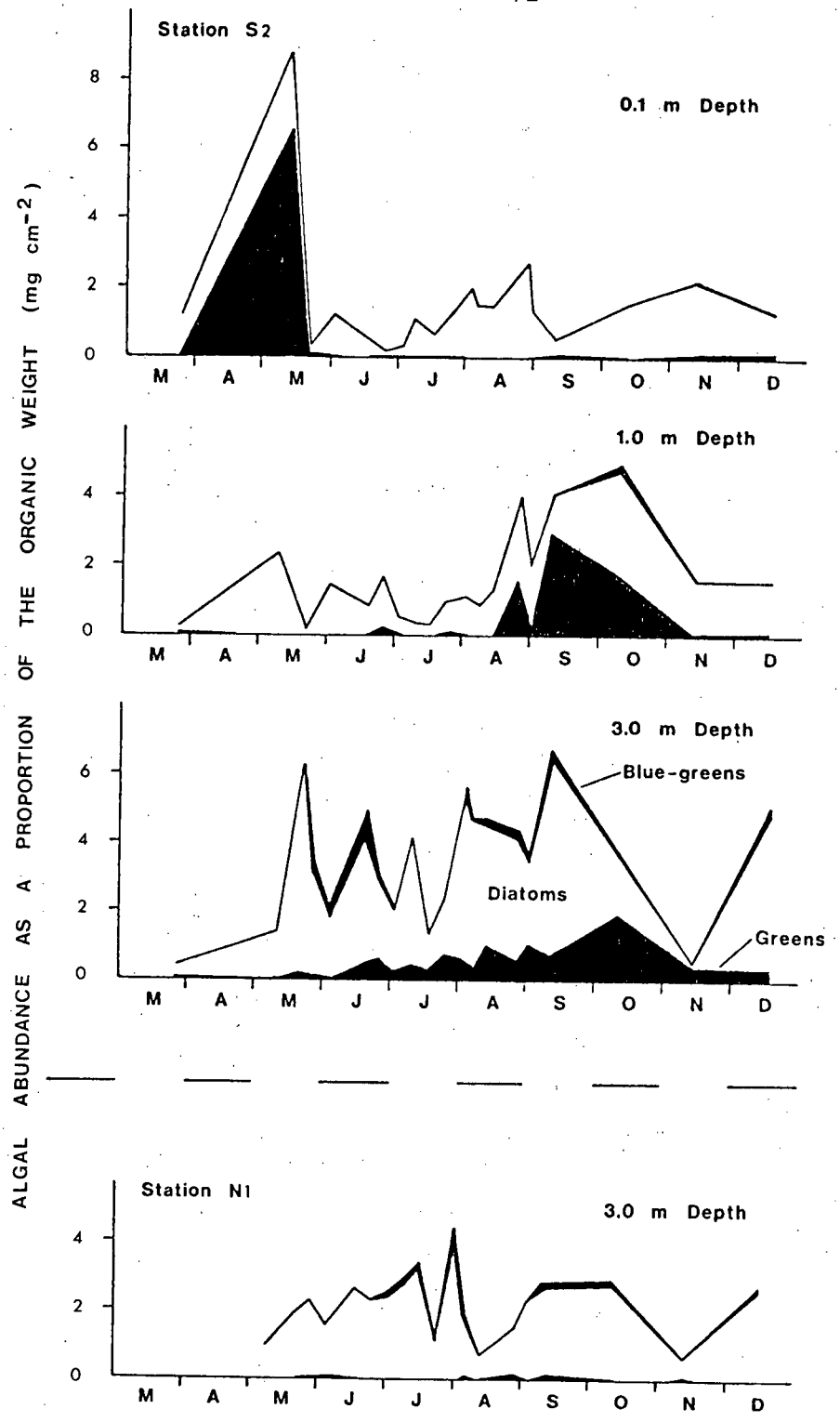


Fig. 33. Seasonal succession in the percentage abundance (by volume) of diatoms, green algae and blue-green algae expressed as a proportion of the organic weight (mg cm^{-2}) at selected depths in the south arm and north arm of Kootenay Lake, 1973.

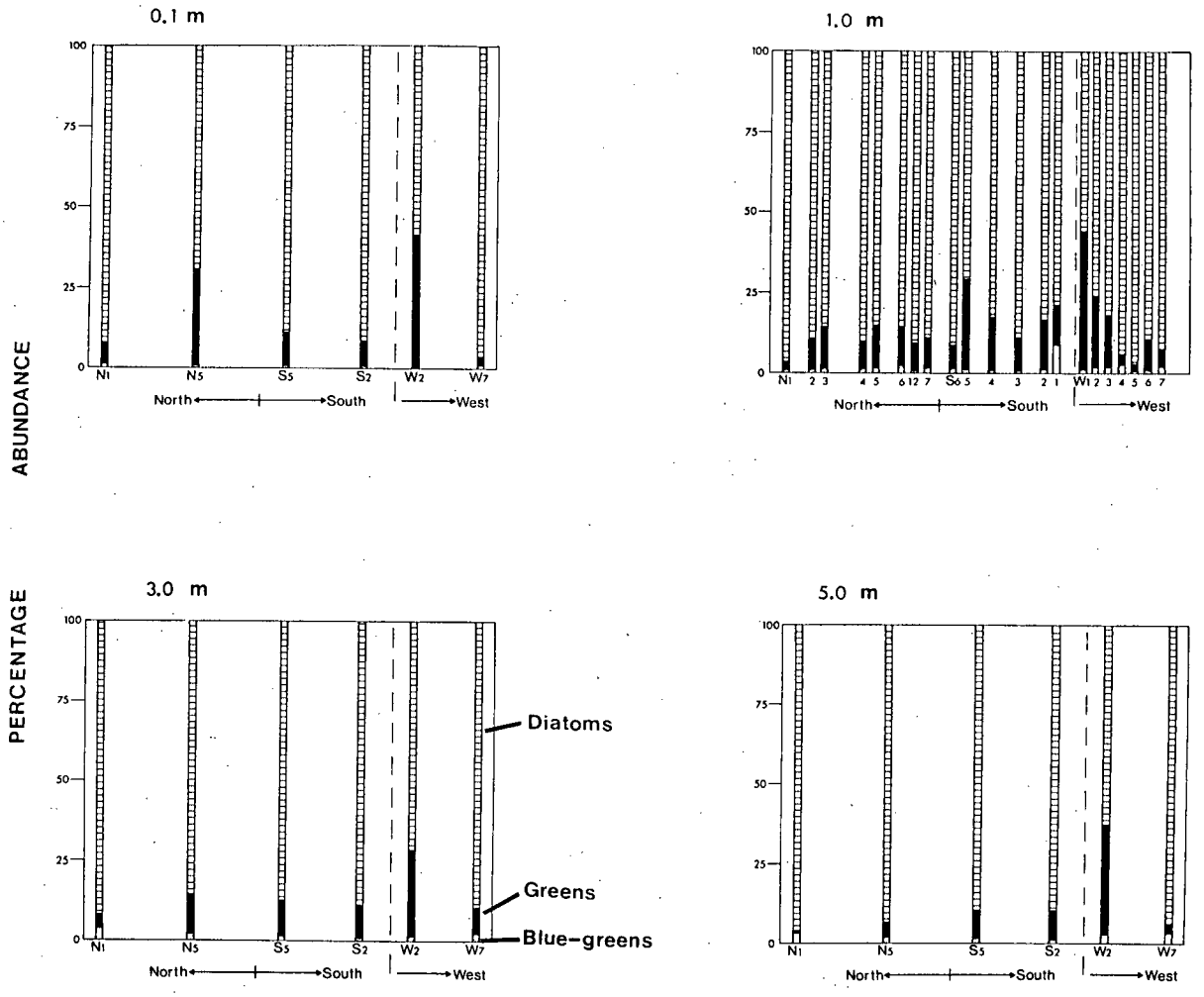


Fig. 34. Regional variations in average percentage abundance (by volume) of diatoms, green algae, and blue-green algae attached to artificial substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973.

Major features, to be sure, were similar, with diatoms being the most abundant group, green algae less abundant and blue-green algae least abundant. But the levels of abundance and trends in regional variation usually differed from those observed for natural populations of attached algae.

Diatoms, with some exceptions, formed about 90 percent (by volume) of the attached algal biomass at all depths (Fig. 34). Station W1 had fewer diatoms than the other stations, but otherwise little regional variation occurred. Green algae likewise exhibited few regional trends, with an average abundance of about 10 percent except at station W1 where they were more abundant. At the deeper depth *Cladophora* did not grow on the artificial substrates, so there was no increase in green algae southwards, as observed on natural substrates (Fig. 35). Green algae, other than *Cladophora*, were more abundant on plexiglas than on the rock substrates. As a result, the south arm showed similar proportions of green algae (total algal abundance) on both kinds of substrate, while the north arm (where *Cladophora* did not grow naturally) showed larger proportions of green algae on the plexiglas substrates. Blue-green algae, forming less than two percent of the community biomass, were even less common on plexiglass than on rocks. There was no increase in blue-green abundance along the length of the west arm, contrary to the pattern observed on natural rock substrates at all depths.

Species Composition

1. Green Algae

Owing to the general lack of green algae throughout the year (Fig. 33) and the difficulty in accurately enumerating the filamentous species, cell

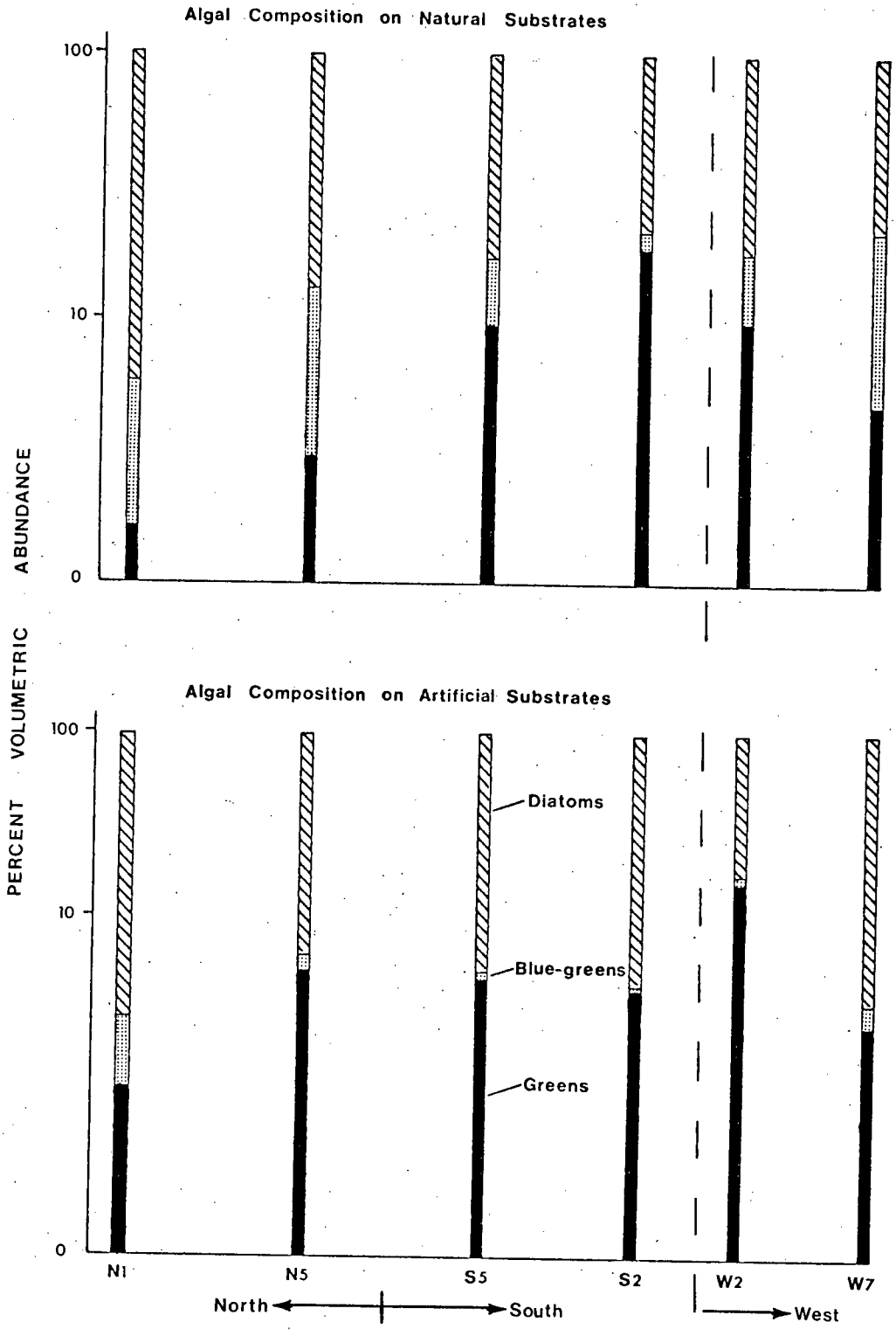


Fig. 35. Average percentage composition (by volume) of diatoms, green algae, and blue-green algae on natural rock substrates compared to that on artificial substrates at 3.0 m in Kootenay Lake, 1973. Note logarithmic scale.

counts were not performed and parameters such as diversity therefore could not be calculated. However, while identifying the green algal species and estimating the percentage abundance of the algal groups, I was able to appraise the importance of each green algal species at the various sampling locations and sampling times. In all, twenty-four species of green algae were identified from Kootenay Lake's attached algal assemblages (Table II). Many of the features of green algae, as a whole, were discussed in the previous section.

Most of the green algal species exhibited little regional variation. *Ulothrix aequalis* Kütz., and *U. tenuissima* which formed the spring growth peak and *Spirogyra* spp. predominant in the fall belonged to this category, being common at all locations in the lake. *Oedogonium* spp. and *Elakatothrix* sp. which were moderately abundant were also widespread. Most other green algal species occurred in small numbers but appeared to be present in all regions of Kootenay Lake.

Cladophora aegagropila, *Bulbochaete* sp. and *Rhizoclonium* sp., unlike the other green algal species, were associated with particular regions of the lake. *Cladophora aegagropila*, a shade-loving species flourishing in eutrophic water (Hoek, 1963), was common in the south arm of the lake and at some west arm stations, but was seldom encountered in the north arm (Fig. 36). In the south arm *C. aegagropila* had an upper growth limit at the 2.5 m depth, peaked at 3-5 m then gradually disappeared and was not present at the 10.0 m depth. As previously mentioned, *C. aegagropila* never grew on artificial substrates, being restricted to the natural rock habitat. In contrast, *Bulbochaete* sp. was only enumerated in the artificial substrate samples,

Table II. A list of the attached algal species, except diatoms, occurring in the littoral zone of Kootenay Lake.

Chlorophyta:

Ankistrodesmus falcatus (Corda) Ralfs
**Bulbochaete* sp.
Coelastrum microporum Naegali
Chlamydomonas sp.
Cosmarium sp.
Cladophora aegagropila (L.) Rabh.
Dictyosphaerium sp.
Elakatothrix sp.
Gloeocystis ampla (Kütz.) Lagerheim
Gongrosira sp.
Oedogonium spp.
Oocystis sp.
Pediastrum duplex Meyen
Rhizoclonium sp.
Scenedesmus sp.
Spirogyra sp.
Spondylosium sp.
Ulothrix aequalis Kütz.
Ulothrix tenuissima Kütz.
Ulothrix zonata (Weber & Mohr)' Kütz.
Unidentified Desmidiaceae
Unidentified spp.
Unidentified Volvocales sp.
Zygnema sp.

Cyanophyta:

Anabaena flos-aquae (Lyngb.) De Bréb.
Anabaena circinalis Rabh.
Anacystis sp.
Aphanocapsa sp.
Calothrix sp.
Chroococcus sp.
Coelosphaerium sp.
Gomphosphaeria sp.
Lyngbya nordgaardii Wille
Lyngbya spp.
Merismopedia sp.
Microcystis sp.
Nostoc sp.
Oscillatoria spp.
Phormidium sp.
Rivularia sp.
Sacconema rupestre Borzi
Spirulina sp.
Tolypothrix distorta Kütz.
Unidentified colonial form

Pyrrhophyta:

Peridiniopsis penardii (Lemm.) Bourr.

Cryptophyta:

Cryptomonas borealis (Skuja)

Chrysophyta-Chrysophyceae:

Mallomonas sp.

*Occurred on plexiglas substrates only.

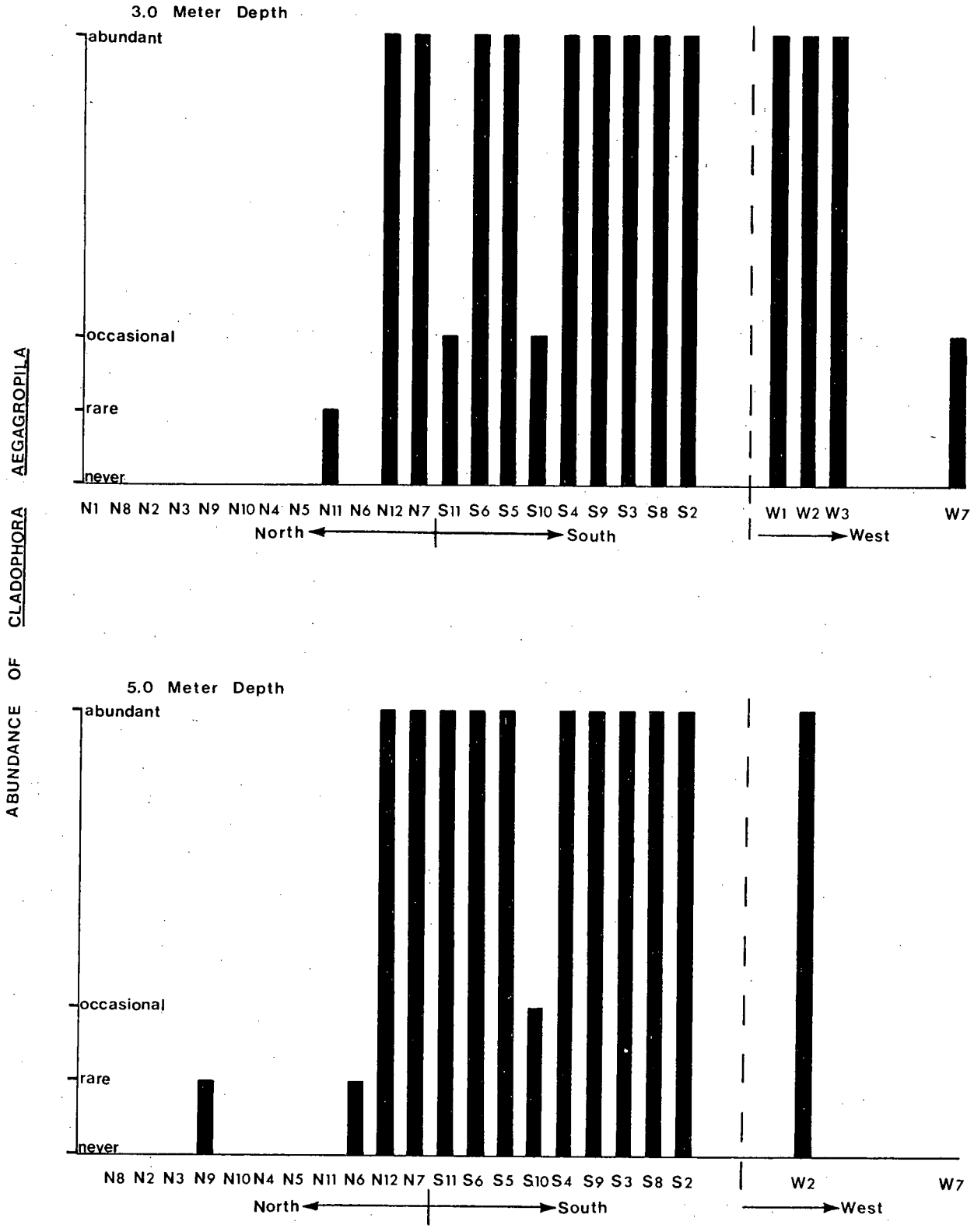


Fig. 36. Regional variations in the average abundance of *Cladophora aegagropila* attached to natural rock substrates at 3.0 and 5.0 m in Kootenay Lake, 1973. Absence of vertical bars at a station indicates the alga was never encountered.

although there must have been small amounts present on the natural substrates. This species was also restricted to the south and west arms of the lake, as was *Rhizoclonium* sp.

2. Blue-green Algae

Because of their small populations, the twenty species of blue-green algae identified in this study (Table II) were not enumerated individually. The abundance of the entire group is discussed in the previous section. *Lyngbya nordgaardii* Wille and *Oscillatoria* spp. were the most frequent and widespread species. *Calothrix* sp., *Phormidium* sp., *Sacconema rupestre* Borzi, and *Tolypothrix distorta* Kütz. were often present in the west arm, and less frequently encountered elsewhere. Others were found occasionally, although some, such as *Nostoc* sp., formed a large proportion of the attached algal biomass when they did occur.

Attached Diatoms

Diatoms formed the major portion of the attached algal community and were therefore examined in detail. The diatom species were identified (in many cases to the subspecies level) as well as enumerated for cell counts and cell volumes. The following sections present results in terms of diatom cell numbers, cell volumes, numbers of species, diversity, station clusters based upon diatom distributions, and species distributions.

1. Diatom Abundance

i. Natural Substrates

Yearly and seasonal mean diatom numbers ranged from about

1×10^5 to 9×10^6 cells cm^{-2} of rock surface (Fig. 37). Cells increased with depth, ranging from approximately 1×10^6 diatoms per cm^2 near the lake surface, to counts generally greater than 3×10^6 cells cm^{-2} at the 5.0 m depth. At all depths, spring numbers tended to be highest and summer counts lowest. Station N5 at the 3.0 and 5.0 meter depths had an immense number of diatoms during spring, 8.5×10^6 cells cm^{-2}, much more than observed elsewhere. Consistent regional trends in cell numbers were not detectable at any depth, the seasonal variation at specific locations being far greater than most differences between stations.

Total cell volumes for each station were calculated by multiplying cell count by average volume for each species (Table III) and summing the results for all species in the sample. Yearly and seasonal average diatom cell volumes (not including gelatinous sheaths and stalks) ranged from about 0.5 mm^3 to 4 mm^3 per cm^2 of rock surface (Fig. 38). Cell volumes were not consistently greater at the deeper depths (as numbers were), indicating that the diatoms near the lake surface were larger. Seasonal variation in cell volumes, as observed with cell counts, was generally greater than regional variation. The 5.0 m depth was an exception, greater diatom volumes occurring in the less turbid north arm (Fig. 9) than at other locations.

ii. Artificial Substrates

Cell counts and volumes from artificial substrates cannot be directly compared to abundance on rocks. Both plexiglas grown cell numbers and volumes (accumulated in two weeks) are considerably less than those accumulated on rocks over an unknown but undoubtedly longer period of time.

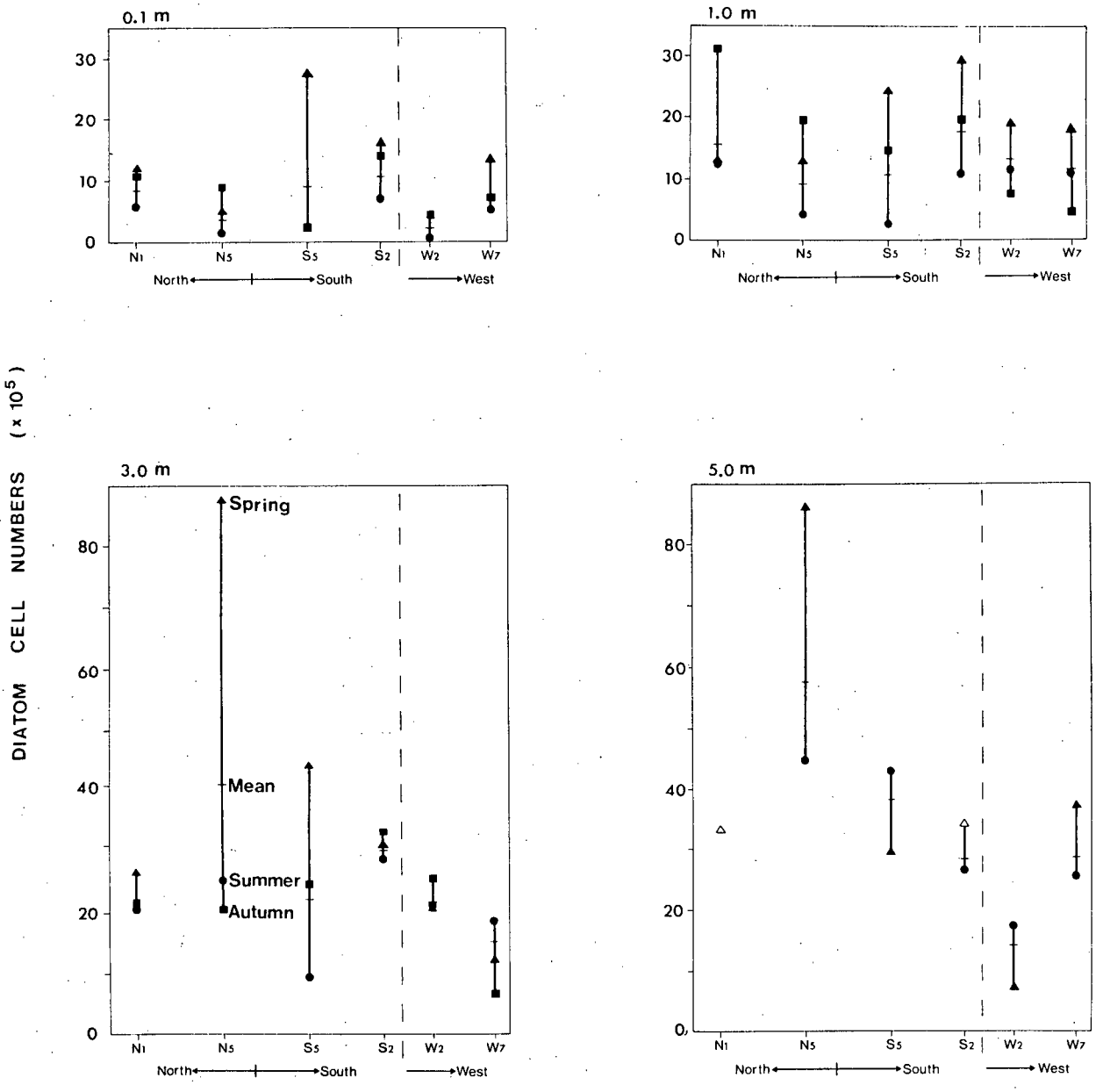


Fig. 37. Regional variations in average diatom cell numbers ($x10^5$) attached to natural rock substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Horizontal bars represent yearly averages, solid symbols represent seasonal averages and open symbols represent single measurements.

Table III. A list of the attached diatom species, their cell volumes and numeric and volumetric occurrence on natural and/or artificial substrates in the littoral zone of Kootenay Lake. For occurrence; open circles (o) denote a species always made up less than 10% of a sample's abundance, solid circles (●) denote that a species made up greater than 10% of at least one sample's abundance. If a species has no record for occurrence that species was never encountered during quantitative diatom analyses but does occur in the attached flora.

	Bacillariophyceae Species	Cell Volume (μm^3)	Occurrence: Natural Substrates Numeric	Natural Substrates Volumetric	Artificial Substrates Numeric	Artificial Substrates Volumetric
	Coscinodiscales:					
1	*Cyclotella atomus* Hust.	20	o	o	o	o
2	*Cyclotella comta* (Ehr.) Kütz.	400	o	o	o	o
3	*Cyclotella glomerata* Bachm.	20	●	o	●	o
4	*Cyclotella kuetzingiana* Thwaites	100	o	o	o	o
5	*Cyclotella meneghiniana* Kütz.	160	o	o		
6	*Cyclotella ocellata* Pant.	180	o	o	o	o
7	*Cyclotella pseudostelligera* Hust.	50	o	o	o	o
8	*Cyclotella* sp.	110	o	o		
9	*Cyclotella stelligera* Cl. & Grun.	50			o	o
10	*Cyclotella striata* (Kütz.) Grun.	50	o	o	o	o
11	*Cyclotella vorticosa* A. Berg.	120			o	o
12	*Coscinodiscus lacustris* Grun.	410	o	o	o	o
13	*Melosira arenaria* Moore	41560	o	●		
14	*Melosira binderana* Kütz	200	●	o	o	o
15	*Melosira granulata* (Ehr.) Ralfs	1780	o	o	o	o
16	*Melosira islandica* O. Müll.	530	o	o	o	o
17	*Melosira varians* Ag.	5260	o	●	o	●
18	*Stephanodiscus astraea* (Ehr.) Grun.	1240	●	●	●	●
19	*Stephanodiscus astraea* var. *minutula* (Kütz.) Grun.	110	●	●	●	●
20	*Stephanodiscus dubius* (Fricke) Hust.	90	o	o	o	o
21	*Stephanodiscus hantzschii* Grun.	110	o	o	o	o
	Rhizosoleniales:					
22	*Rhizosolenia eriensis* H.L. Sm.	180	o	o	o	o
	Fragilariales:					
23	*Asterionella formosa* Hass.	270	●	●	●	●
24	*Diatoma anceps* (Ehr.) Kirchn.	280	o	o	o	o
25	*Diatoma hiemale* (Lyngb.) Heib.	520	o	o	o	o
26	*Diatoma tenue* Ag.	250	●	●	●	●
27	*Diatoma vulgare* Bory	2290	●	●	o	o
28	*Fragilaria capucina* Desm.	760	●	●	●	●
29	*Fragilaria constricta* Ehr.	200	o	o		
30	*Fragilaria construens* (Ehr.) Grun.	150	●	●	●	●
31	*Fragilaria construens* var. *binodis* (Ehr.) Grun.	180	●	●	●	●
32	*Fragilaria construens* var. *venter* (Ehr.) Grun.	80	●	●	●	●
33	*Fragilaria crotonensis* Kitton	530	●	●	●	●
34	*Fragilaria heiden* Östr.	140	o	o	o	o
35	*Fragilaria leptostauron* (Ehr.) Hust.	880	o	●	o	o
36	*Fragilaria pinnata* Ehr.	170	●	o		
37	*Fragilaria vaucheriae* (Kütz.) Peters.	380	●	●	●	●
38	*Hannaea arcus* (Ehr.) Patr.	1260	o	o	o	o
39	*Opephora martyi* Hérib.	270	●	●	o	o
40	*Synedra acus* Kütz.	1040	●	●	●	●
41	*Synedra* Cf. *amphicephala* var. *austriaca* (Grun.) Hust.	370	o	o		
42	*Synedra arcuata* (Östr.) A. Cl.	1680	o	o		
43	*Synedra delicatissima* W. Sm.	670	o	o	o	o
44	*Synedra famelica* Kütz.	150	o	o		
45	*Synedra fasciculata* (Ag.) Kütz.	900			o	o
46	*Synedra mazamaensis* Sov.	210	●	o	o	o
47	*Synedra rumpens* Kütz.	1050	●	o		
48	*Synedra* sp.	630	o	o	o	o
49	*Synedra ulna* (Nitz.) Ehr.	6640	●	●	o	●
50	*Tabellaria fenestrata* (Lyngb.) Kütz.	1330	o	●	o	o
51	*Tabellaria flocculosa* (Roth) Kütz.	430	o	o		
52	Unidentified Araphe	300	o	o		
	Eunotiales:					
53	*Eunotia pectinalis* (Kütz.) Rabh.	1340	o	o	o	o

Table III (Continued)

	Bacillariophyceae Species	Cell Volume (μm^3)	Occurrence: Natural Substrates Numeric	Natural Substrates Volumetric	Artificial Substrates Numeric	Artificial Substrates Volumetric
	Achnanthales:					
54	*Achnanthes* Cf. *bergiana* A. Cl.	190	o	o		
55	*Achnanthes* Cf. *biasolettiana* (Kütz.) Grun.	400	o	o		
56	*Achnanthes calcar* (Cl.) Cl.	190	o	o	o	o
57	*Achnanthes clevei* Grun.	220	●	o	●	o
58	*Achnanthes clevei* var. *rostrata* Hust.	220	o	o	o	o
59	*Achnanthes divergens* A. Cl.	80				
60	*Achnanthes exigua* Grun.	130	o	o	o	o
61	*Achnanthes flexella* (Kütz.) Brun	90	o	o	o	o
62	*Achnanthes* Cf. *inflata* (Kutz.) Grun.	500	o	o		
63	*Achnanthes lanceolata* (Bréb.) Grun.	190	o	o	o	o
64	*Achnanthes lewisiana* Patr.	50	o	o	●	o
65	*Achnanthes linearis* (W. Sm.) Grun.	180	o	o	o	o
66	*Achnanthes minutissima* Kütz.	60	●	●	●	●
67	*Achnanthes peragalli* Brun & Hérib.	240	o	o	o	o
68	*Achnanthes pinnata* Hust.	140	o	o		
69	*Achnanthes* spp.	200	o	o	o	o
70	*Achnanthes* spp.	200	o	o		
71	*Cocconeis disculus* (Schum.) Cl.	140	o	o	o	o
72	*Cocconeis pediculus* Ehr.	880	o	o	o	o
73	*Cocconeis pellucida* Hantz.	2500			o	o
74	*Cocconeis placentula* Ehr.	610	o	●	o	o
75	*Cocconeis* sp.	860	o	o	o	o
76	*Rhoicosphenia curvata* (Kütz.) Grun.	760	●	●	●	●
	Naviculales:					
77	*Amphipleura pellucida* (Kütz.) Kütz.	2600	o	o	o	o
78	*Amphora coffaeformis* (Ag.) Kütz.	500	o	o		
79	*Amphora ovalis* Kütz.	320	o	o	o	o
80	*Amphora ovalis* var. *pediculus* (Kütz.) Van Heurck	70	●	o	●	o
81	*Amphora* sp.	640			o	o
82	*Caloneis bacillum* (Grun.) Cl.	450	●	o	o	o
83	*Caloneis hyalina* Hust.	2200	o	o		
84	*Caloneis* Cf. *patagonica* (Cl.) Cl.	2160			o	o
85	*Caloneis silicula* var. *limosa* (Kütz.) Van Lan.	1200			o	o
86	*Caloneis* sp.	1500	o	o	o	o
87	*Cymbella affinis* Kütz.	1300	o	●	o	o
88	*Cymbella aspera* (Ehr.) Cl.	16480	o	●	o	o
89	*Cymbella caespitosa* (Kütz.) Brun	630	●	●	●	●
90	*Cymbella cistula* Hempr.	6850	o	●	o	●
91	*Cymbella heteropleura* Ehr.	10620				
92	*Cymbella prostrata* (Berk.) Cl.	7210	o	●	o	●
93	*Cymbella reinhardtii* Grun.	320	o	o		
94	*Cymbella* sp. "A"	99060	o	●	●	●
95	*Cymbella* sp.	3000	o	o	o	o
96	*Cymbella tumidula* Grun.	1330				
97	*Cymbella turgida* Greg.	890	o	o	o	o
98	*Cymbella ventricosa* Kütz.	100	●	●	●	o
99	*Diploneis decipiens* A. Cl.	920	o	o	o	o
100	*Frustulia rhomboides* (Ehr.) De T.	3840	o	o	o	o
101	*Gomphonema acuminatum* Ehr.	1630	o	o		
102	*Gomphonema constrictum* Ehr.	2080			o	o
103	*Gomphonema geminatum* (Lyngb.) Ag.	Large				
104	*Gomphonema gracile* Ehr.	980	o	o		
105	*Gomphonema herculeanum* Ehr.	13000	●	●	●	●
106	*Gomphonema montanum* var. *subclavatum* Grun.	1390	●	●	●	●
107	*Gomphonema olivaceum* (Lyngb.) Kütz.	470	●	●	o	o
108	*Gomphonema olivaceum* var. *genuinum* f. *minutula* (May.) May.	210	o	●	o	o
109	*Gomphonema parvulum* (Kütz.) Kütz.	560	●	●	●	●
110	*Gyrosigma sciotense* (Sulliv. & Wormley) Cl.	4600			o	●

Table III (Continued)

	Bacillariophyceae Species	Cell Volume (μm^3)	Occurrence: Natural Substrates Numeric	Natural Substrates Volumetric	Artificial Substrates Numeric	Artificial Substrates Volumetric
	Naviculales (cont'd)					
111	*Navicula accomoda* Hust.	60	●	o	●	●
112	*Navicula amphibola* Cl.	2020	o	o	o	o
113	*Navicula anglica* Ralfs	140				
114	*Navicula aurora* Sov.	4200				
115	*Navicula cincta* (Ehr.) Ralfs	310	●	●	o	o
116	*Navicula cocconeiformis* Greg.	720	o	o	o	o
117	*Navicula cryptocephala* Kütz.	660	o	o	o	o
118	*Navicula decussis* Östr.	480	o	o		
119	*Navicula elginensis* (Greg.) Ralfs	620	o	o	o	o
120	*Navicula* Cf. *festiva* Krasske	360	o	o		
121	*Navicula gottlandica* Grun.	1090	o	o		
122	*Navicula graciloides* May.	320	●	●	o	o
123	*Navicula minuscula* Grun.	80	o	o	o	o
124	*Navicula odiosa* Wallace	220	o	o		
125	*Navicula pseudoscutiformis* Hust.	420	o	o	o	o
126	*Navicula pupula* Kütz.	600			o	o
127	*Navicula radiosa* Kütz.	1320	o	●	o	●
128	*Navicula reinhardtii* (Grun.) Grun.	940	o	o	o	o
129	*Navicula salinarum* var. *intermedia* (Grun.) Cl.	810			o	o
130	*Navicula schonfeldii* Hust.	420	o	o	o	o
131	*Navicula scutelloides* W. Sm.	290	o	o	o	o
132	*Navicula* spp.	140	o	o	o	o
133	*Navicula* spp.	140	o	o	o	o
134	*Navicula* spp.	140	o	o	o	o
135	*Navicula tripunctata* (O. Müll.) Bory	1600	o	o	o	●
136	*Pinnularia biceps* Greg.	3960				
137	*Pinnularia* sp.	3900	o	●	o	o
138	*Stauroneis anceps* Ehr.	600	o	o		
139	*Stauroneis* sp.	600				
140	Unidentified Raphe	400	o	o		
	Surirellinees:					
141	*Cymatopleura solea* (Bréb) W. Sm.	3360				
142	*Denticula elegans* Kütz.	400			o	o
143	*Epithemia sorex* Kütz.	820	●	●	●	●
144	*Epithemia turgida* (Ehr.) Kütz.	16100	●	●	●	●
145	*Epithemia zebra* (Ehr.) Kütz.	1880	o	o		
146	*Hantzschia amphioxys* (Ehr.) Grun.	1310				
147	*Nitzschia acicularis* W. Sm.	300				
148	*Nitzschia actinastroides* (Lemm.) V. Goor.	620	o	●	●	●
149	*Nitzschia affinis* Grun.	900	o	o		
150	*Nitzschia angustata* (W. Sm.) Grun.	1260	o	o	o	o
151	*Nitzschia dissipata* (Kütz.) Grun.	560	●	●	●	●
152	*Nitzschia fonticola* Grun.	110	o	o		
153	*Nitzschia frustulum* (Kütz.) Grun.	150	●	●	●	●
154	*Nitzschia hantzschiana* Rabh.	680	●	●	●	●
155	*Nitzschia heufleuriana* Grun.	960				
156	*Nitzschia linearis* W. Sm.	1650	o	●		
157	*Nitzschia regula* Hust.	1710	o	o		
158	*Nitzschia sigmoidea* (Ehr.) W. Sm.	3840	o	●	o	o
159	*Nitzschia sinuata* (W. Sm.) Grun.	200	o	o	o	o
160	*Nitzschia* sp. "X"	540	o	o		
161	*Nitzschia* sp.	790	o	o		
162	*Rhopalodia gibba* (Ehr.) O. Müll.	8920	o	●	●	●
163	*Rhopalodia gibberula* (Ehr.) O. Müll.	600	o	o		
164	*Surirella helvetica* Brun	12600	o	●	o	●
	Unknown:					
165	**Unidentified**	200	o	o		

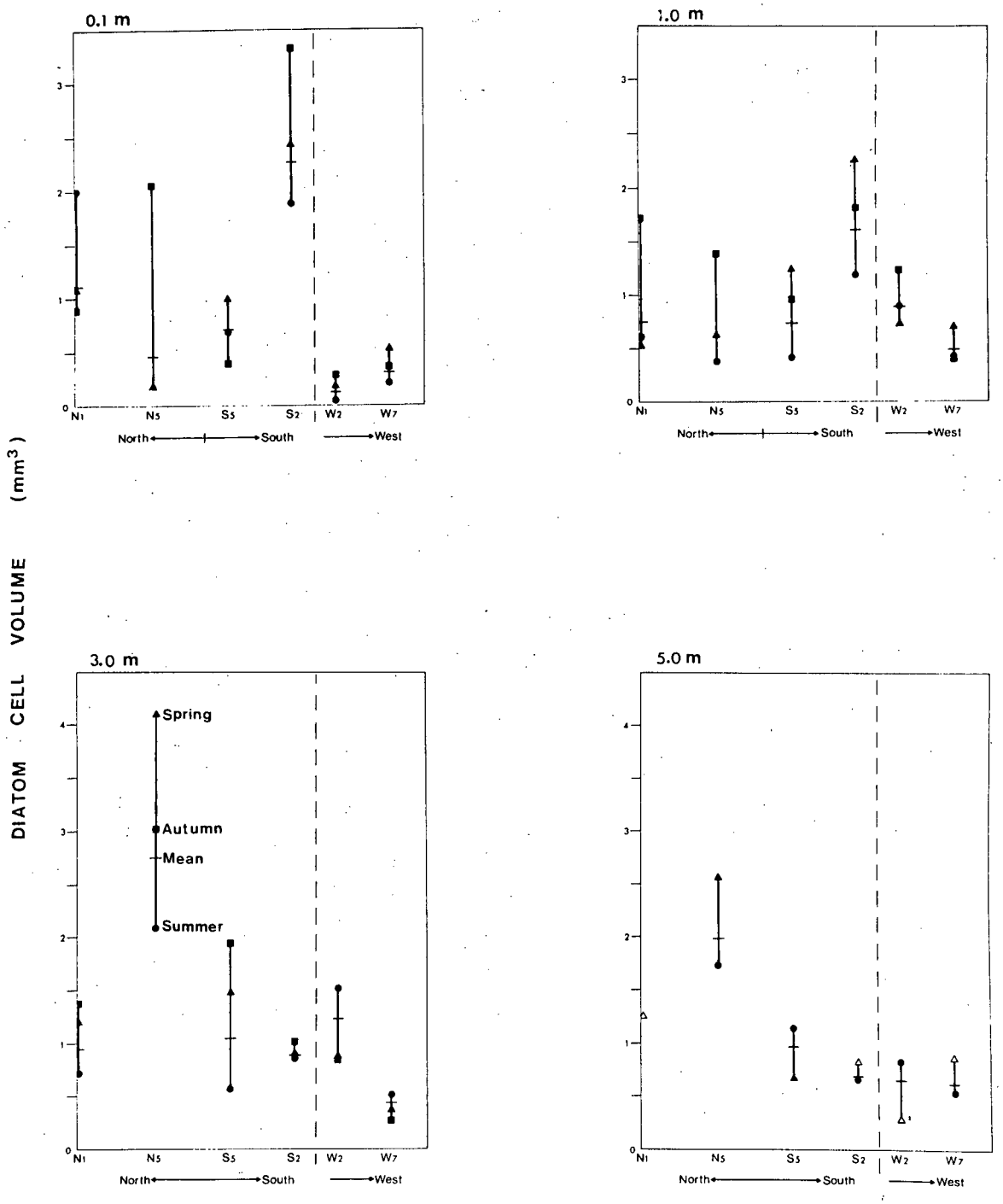


Fig. 38. Regional variations in average diatom cell volumes (mm^3) attached to natural rock substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Horizontal bars represent yearly averages, solid symbols represent seasonal averages and open triangles represent single samples.

Diatom cell numbers (Fig. 39) paralleled organic weight (production) results (Fig. 31). At the shallow depths, diatoms increased from about 2×10^5 cells per cm^2 in the north arm to over 3.5×10^5 cells cm^{-2} in the south arm. At the 3.0 m depth diatom numbers were over 3.5×10^5 cm^{-2} in the north arm, but decreased in the south arm. The 5.0 m depth had lowest numbers of diatoms with values near 1.5×10^5 cm^{-2} everywhere, values in the north arm being only slightly higher than south and west arm values.

Trends in the vertical pattern of diatom numbers on artificial substrates differed from those observed on natural substrates. Though more diatoms are produced at the shallow depths, natural assemblages contain fewer diatoms there than at the deeper depths. Likewise, despite the slower diatom growth rates at the deeper depths, particularly in the south arm, populations increase to high levels. The slower growth rates at the deeper depths are probably related to less light energy. Greater diatom numbers in the north arm, where more light reached the deeper depths (Fig. 9), support this contention.

Cell volumes on the artificial substrates (Fig. 40) exhibited similar trends in vertical and regional variation to those observed for cell numbers on the artificial substrates. Diatom volumes generally decreased with depth. At the shallow depths, volumes were highest in the south arm (over 0.2 mm^3 cm^{-2}) and lowest in the north arm (under 0.2 mm^3 cm^{-2}). At the 3.0 m depth, north arm stations had over 0.1 mm^3 cm^{-2} while south arm stations had less than 0.1 mm^3 cm^{-2}. There were no apparent trends at the 5.0 m depth, with values ranging from approximately 0.02 to 0.11 mm^3 cm^{-2} of rock surface.

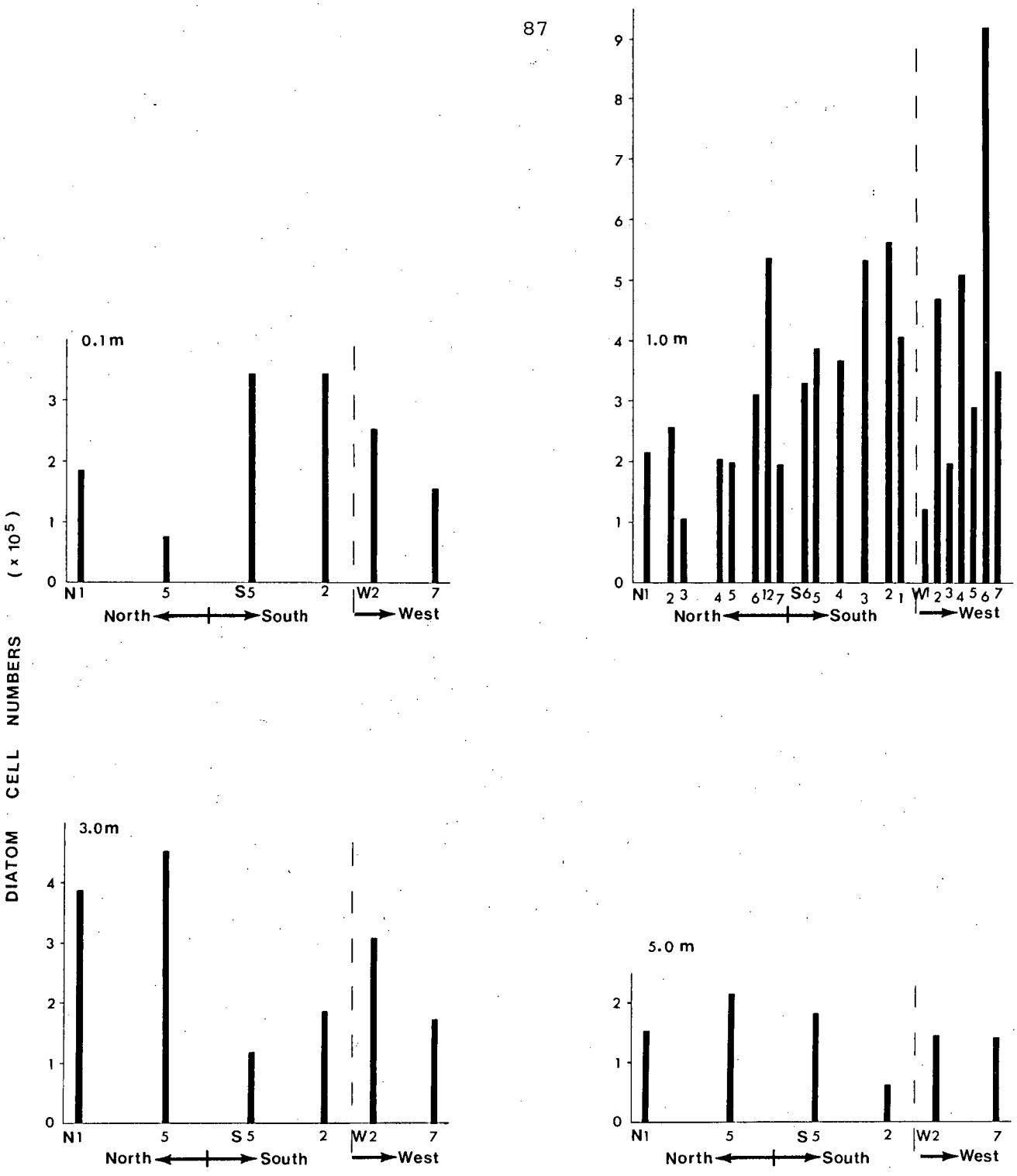


Fig. 39. Regional variations in average diatom cell numbers ($x10^5$) attached to artificial substrates, after two weeks' growth, at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973.

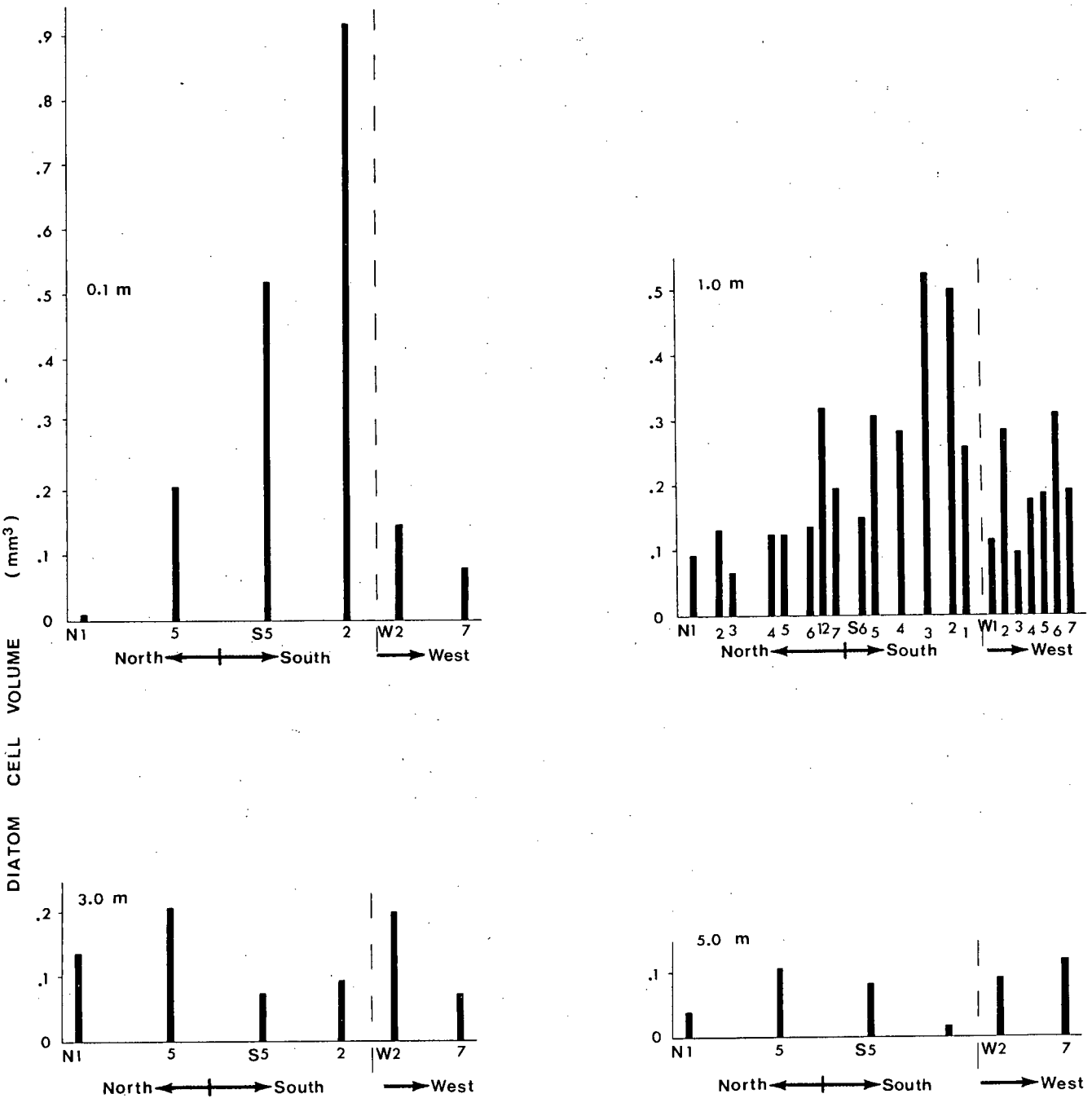


Fig. 40. Regional variations in average diatom cell volumes (mm^3) attached to artificial substrates, after two weeks' growth, at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973.

2. Diatom Diversity

i. Natural Substrates

The average number of diatom species identified per sample ranged from about 10 to 30 species (Fig. 41). The number of species was least near the lake surface (about 10-15 species) and greatest at the 3.0 and 5.0 m depths. Regional variations in the numbers of species were not apparent. The number of different species encountered, at each station, during the entire study ranged from about 40 to 70 species (Fig. 41). Again, species numbers were least near the surface and greatest at the 3.0 and 5.0 m depths, with no apparent regional variation. Results are not easily comparable to other studies since the number of species identified is related to the effort spent in enumerating individual samples.

A measure of diatom species diversity which depends on both the number of taxa and abundance of individuals within each taxa was also calculated. This index, called the Shannon-Wiener function, produces results that are easily compared with other studies. The sampling effort has less influence on the results because increases in the number of rare species are offset by the greater abundance of individuals in the common species. The Shannon-Wiener function H', ($H' = \sum_{i=1}^{n} Pi \log_2 Pi$, where n = number of species and p = proportion of the total sample belonging to the i^{th} species) ranges from values below 1 for low diversity (often polluted) waters (Weber, 1973) to values as high as 3 or 4 in unpolluted waters.

In Kootenay Lake, average Shannon-Wiener diversities of the attached algal community range from 2.5 to 3.5 (Fig. 42). Diversity in the north arm of the lake is greater than in the south arm, except at the lake

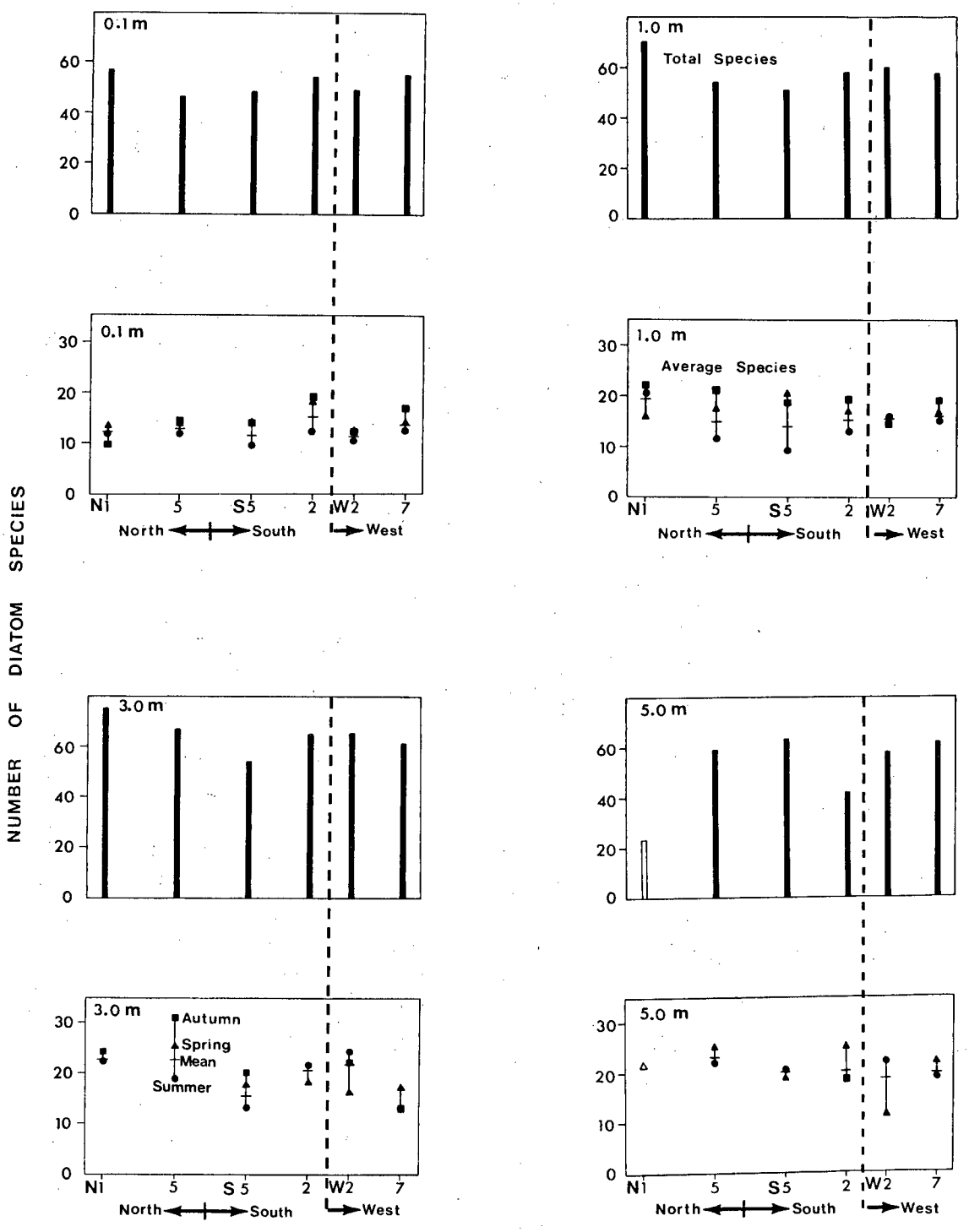


Fig. 41. Regional variations in the average number of diatom species attached to natural substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake 1973. Vertical bars represent the total number of species identified during the entire study. Horizontal bars represent yearly averages, solid symbols represent seasonal averages and open triangles represent single samples.

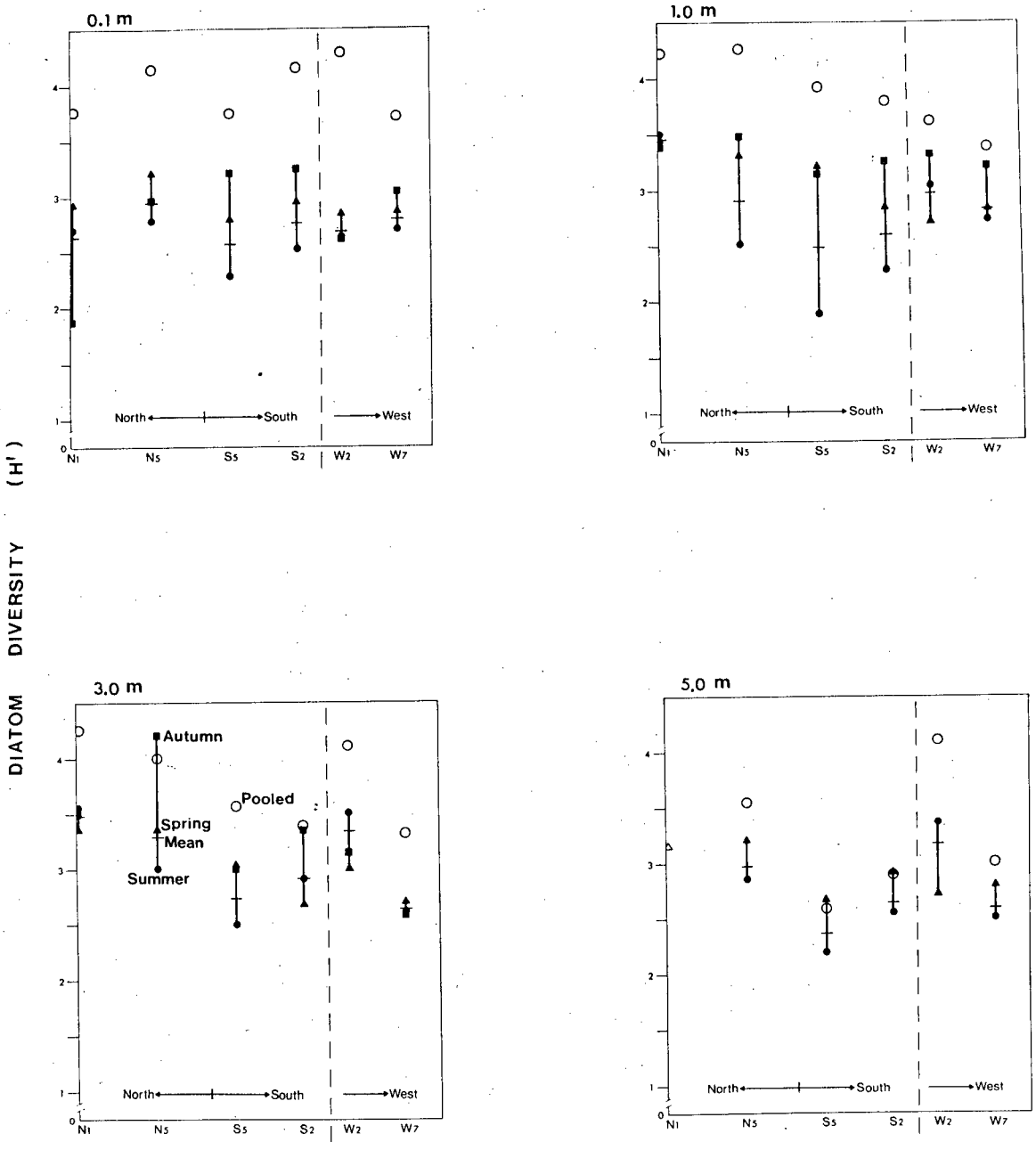


Fig. 42. Regional variations in average diatom diversity (Shannon-Wiener function, H') on natural rock substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Large open circles represent diversities calculated after pooling all the species counts for the entire sampling period. Horizontal bars represent yearly averages, solid symbols represent seasonal averages and open triangles represent single samples.

surface where trends are not apparent.

Shannon-Wiener diversity indicies were also calculated for each station, after pooling all the species counts from the individual samples collected throughout the year. These pooled diversities would correct for any erratic individual samples which could affect the yearly mean diversities presented above. Furthermore, unlike yearly mean diversities, yearly pooled diversities would be lower in polluted regions where a few pollution tolerant species persist throughout the year. In Kootenay Lake yearly pooled diversity values (3.5 to 4.5) are higher than average values (Fig. 42), indicating that the lake is not badly polluted. North arm diversities are again higher than south arm diversities, except at the lake surface where there is no apparent pattern.

ii. Artificial Substrates

The average number of diatom species identified on the artificial substrates ranged from about 10 to 20 species (Fig. 43). The number of taxa on the artificial substrates was generally lower than observed for natural assemblages, probably because of the shorter (two-week) immersion period. As observed with natural substrates, consistent regional variations in the number of taxa were not apparent. The number of different species encountered during the entire study generally ranged from about 40 to 50 species with no apparent regional trends (Fig. 43).

Shannon-Wiener diversity values were similar (2.5 to 3.5) to those observed for natural assemblages (Fig. 44). Trends in diversity were less obvious, with diversities from the 5.0 m depth alone showing consistent northward increases. Pooled diversities were usually between 3.0 and 4.5 with

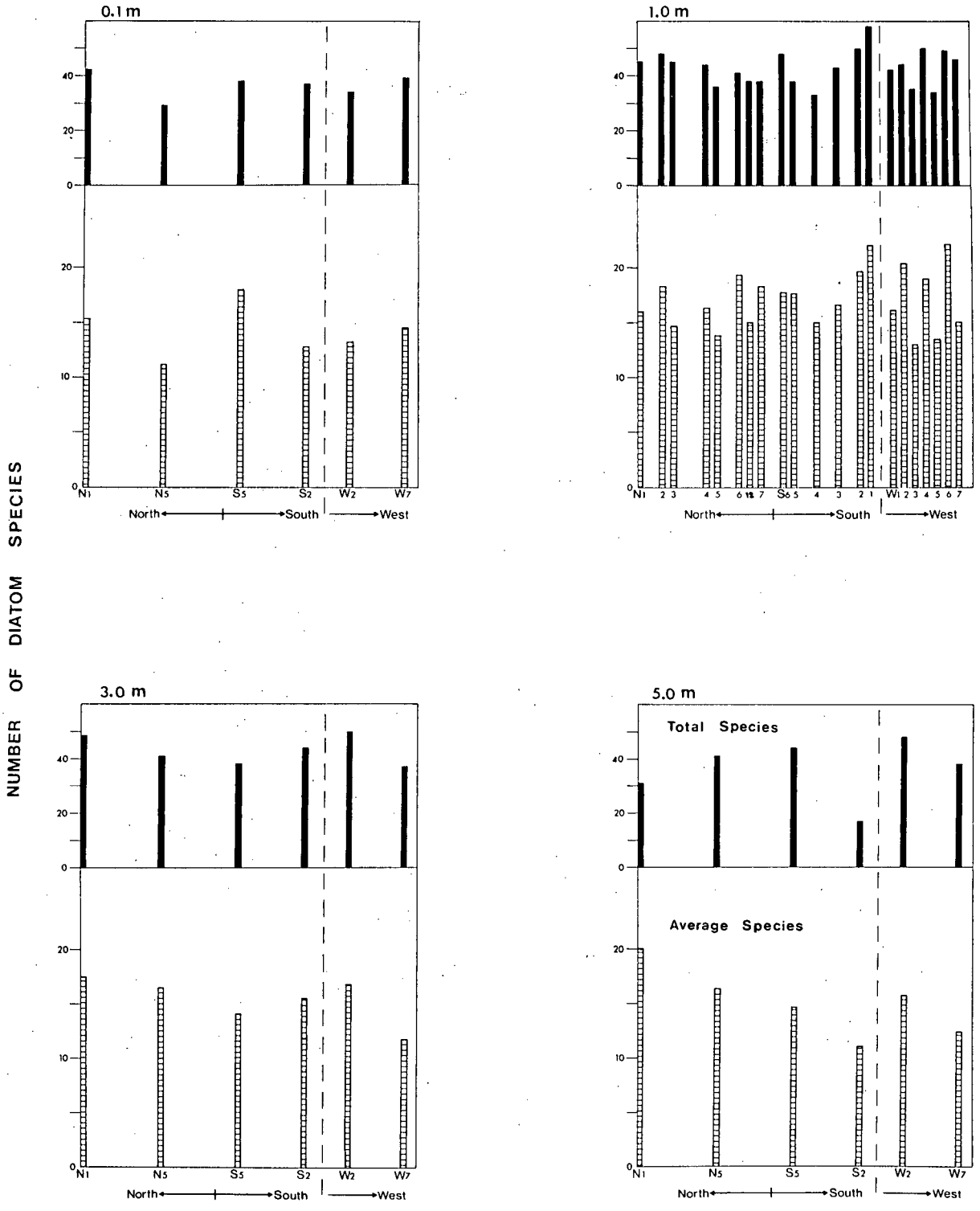


Fig. 43. Regional variations in the average number of diatom species attached to artificial substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Solid vertical bars represent the total number of species identified during the entire study. Hatched vertical bars represent yearly averages.

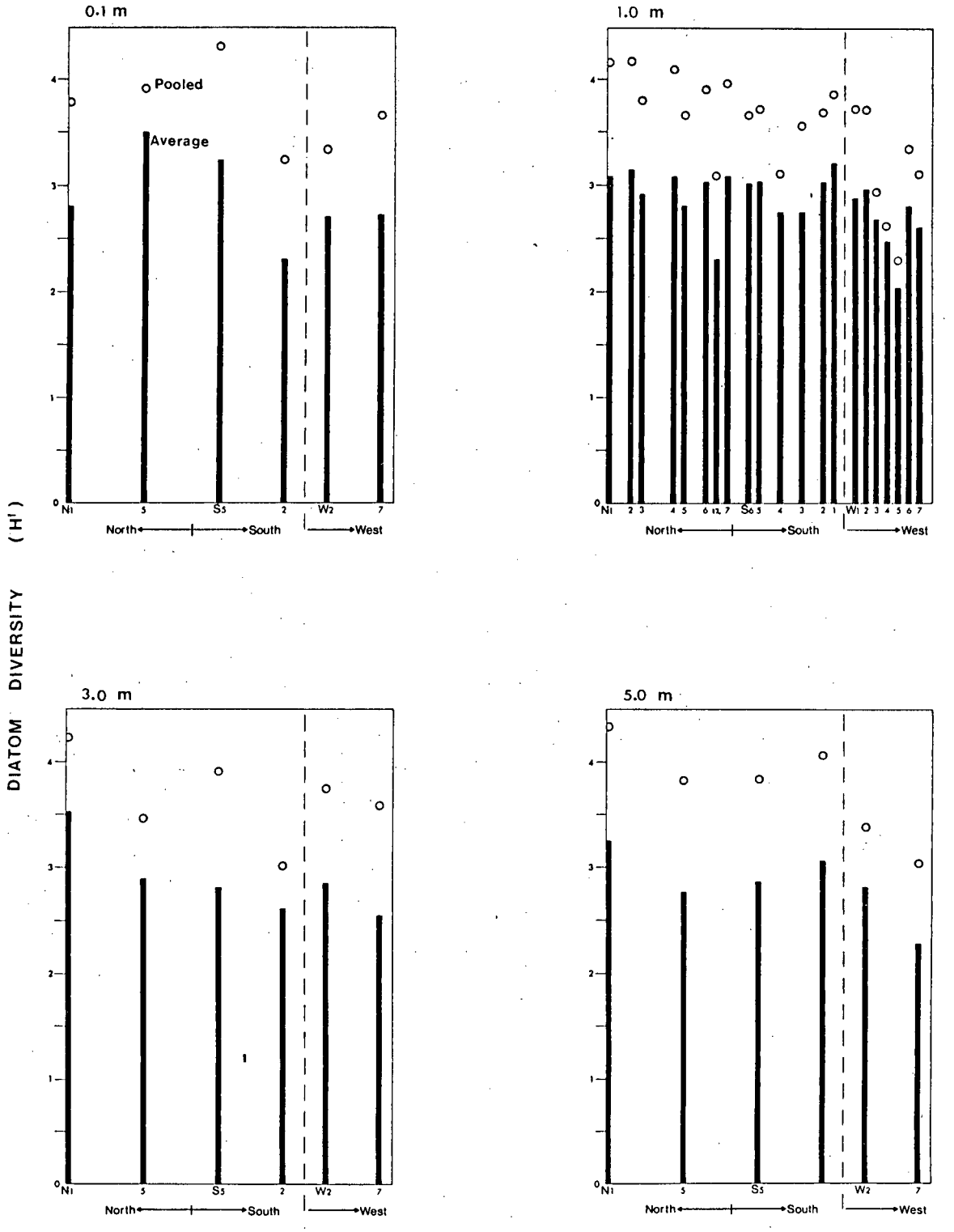


Fig. 44. Regional variations in average diatom diversity (Shannon-Wiener function, H') on artificial substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. Large open circles represent diversities calculated after pooling all the species counts for the entire sampling period. Solid vertical bars represent yearly averages.

generally high values in the north end of the lake (Fig. 44).

3. Diatom Cluster Analyses

A sum of squares amalgamation cluster analysis (U.B.C. Computing Center, MS 1973) was performed to group together similar Kootenay Lake stations. This multivariate technique quantitatively uses all the diatom data to form clusters of similar stations. Three cluster analyses for each substrate type were computed, using numerical counts, numerical percentage abundance and volumetric percentage abundances of the 59 species that formed 10 percent or more of the diatom abundance at any one time (closed circles, Table 3).

i. Natural Substrates

When diatom counts from the 0.1, 1.0, 3.0 and 5.0 m depths of the six major stations were clustered, three groups of stations with high within-group diatom similarities became evident (Fig. 45, top). One group consisted almost entirely of samples from 0.1 and 1.0 m where light levels, turbulence and risks of exposure are great. The 3.0 and 5.0 m depths of all stations were included in the other two major groups. In all groups there was a slight tendency for stations from the same major region of the lake to be clustered together, indicating that highest similarities of diatom distributions usually occur within one lake region.

Clusters based upon numerical percentage abundances produced four major groups of stations (Fig. 45, middle). With some exceptions, the shallow depths again clustered separately from the deeper depths. Interest-

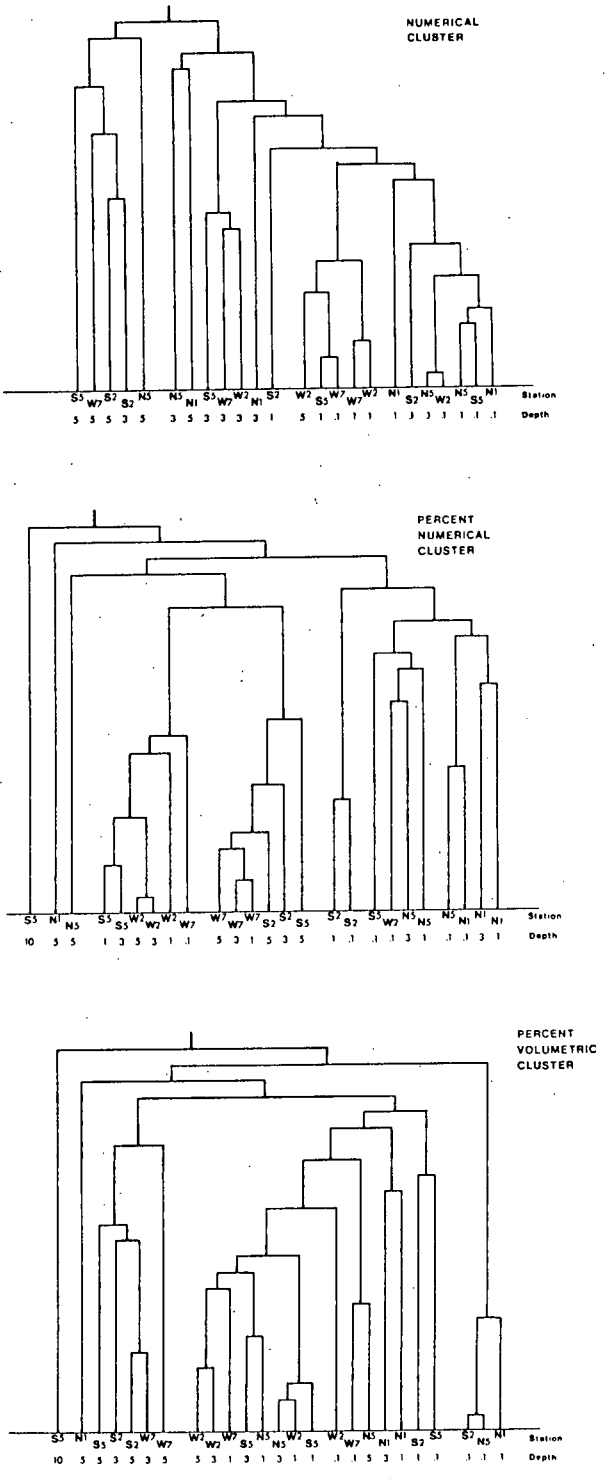


Fig. 45. Station clusters based upon average diatom abundances on natural rock substrates at 0.1, 1.0, 3.0, 5.0, and 10.0 m in Kootenay Lake, 1973. Top cluster based upon absolute numbers, middle cluster based upon percent numerical occurrence, bottom cluster based upon percent volumetric occurrence.

ingly, shallow stations from the more protected west arm of the lake were more similar to the deeper stations than to the shallow stations in the main lake. Within the clusters, stations from similar regions of the lake were strongly clumped, diatom distributions within one lake region being very similar.

Clusters using volumetric percentage data gave similar results to the other two cluster analyses. Again shallow stations clumped together (Fig. 45, bottom) although there were more exceptions than in the other tests. Within the major cluster groups, highest similarities once more occurred between stations from the same lake region.

ii. Artificial Substrates

Data from the 1.0 m depth of the 21 stations were clustered. Since only data from a single depth was clustered, between depth comparisons could not be made, as in the last section, but the great number of stations allow for a more rigorous assessment of regional differences. When diatom numbers were clustered (Fig. 46, top) three major groups of stations occurred. One group consisted of north arm stations as well as station W1 bordering on the north arm of the lake. Another group contained mainly south arm and some west arm stations. The last group contained two west arm stations and station N12 located near the confluence of the three arms. Almost without exception, stations located nearest one another were tightly clustered indicating that they had very similar diatom floras.

Clusters based upon numerical percentage abundance also formed three main station groups (Fig. 46, middle) roughly corresponding to the

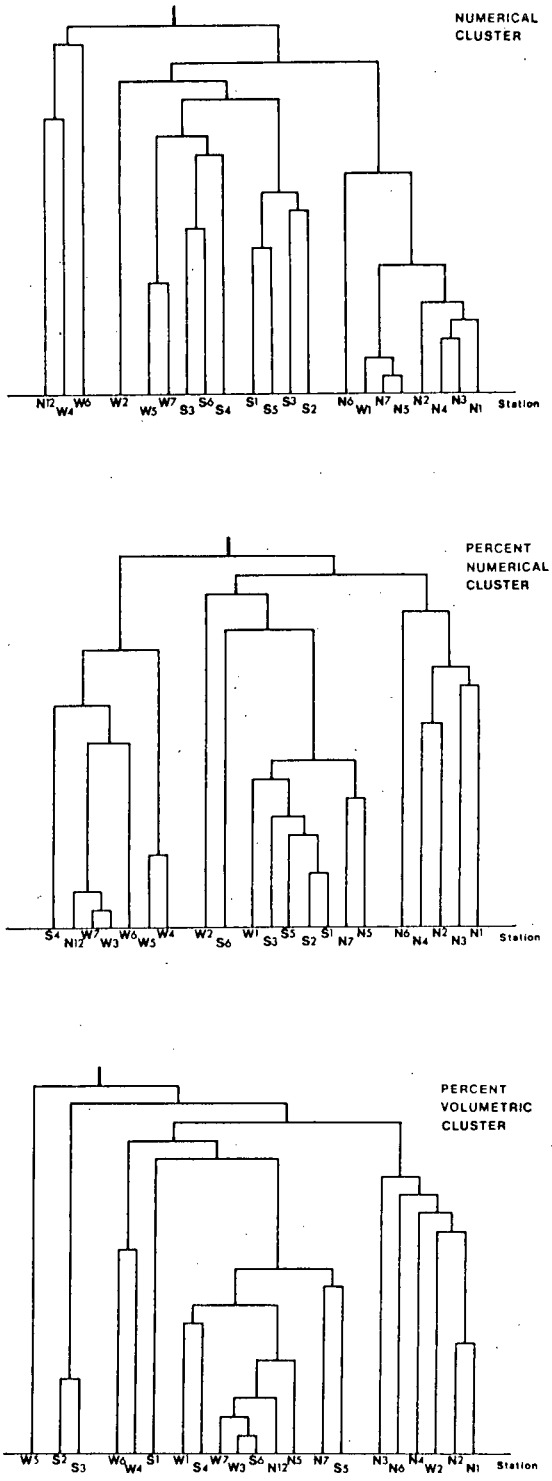


Fig. 46. Station clusters based upon average diatom abundances on artificial substrates at 1.0 m in Kootenay Lake, 1973. Top cluster based upon absolute numbers, middle cluster based upon percent numerical occurrence, bottom cluster based upon percent volumetric occurrence.

three major lake regions. As before, the highest similarities occurred amongst closely located stations.

Clusters using volumetric percentage data also produced three major groups, with results similar to the other two cluster analyses (Fig. 46, bottom). One group consisted almost entirely of north arm stations while the other two groups were less regionally distinct. Nevertheless, nearby stations were tightly clustered, indicating close similarities in their diatom flora.

4. Diatom Species Distributions

In the attached flora of Kootenay Lake there were over 165 diatom species recorded (Table III), of which only 59 made up more than 10 percent of any single sample's numeric and/or volumetric abundance (closed circles, Table III). (It is impossible to tell the actual number of species encountered, since categories such as 'unidentified raphe' may have had different taxa recorded in the individual samples.) When yearly averages were calculated, there were only 34 taxa that made up 5 percent or more of the abundance at the 0.1, 1.0, 3.0 or 5.0 m depths of regularly sampled stations (Fig. 47-50).

Most diatom species belonged to the following orders: Coscinodiscales, Fragilariales, Achnanthales, Naviculales or Surirellinees. The Rhizosoleniales and Eutoniales were also represented in the attached flora (Table III). Although there were 21 diatom species belonging to the Coscinodiscales, the group (except for *Stephanodiscus astraea* and varities) seldom contributed greatly to the attached diatom biomasses. The order Coscinodiscales is generally considered planktonic, and those species observed

may represent individuals that have settled out of the plankton, or else species in the process of increasing their numbers prior to entering the planktonic community (Round, 1971). There were 30 species of Fragilariales identified, many of which formed a large proportion of the diatoms' numeric or volumetric abundance. Achnanthales species, although attached forms, seldom contributed significantly to the flora except for the species *Achnanthes minutissima* Kütz. More than 64 species of Naviculales were identified, and, although individual species were seldom numerically important, large *Cymbella* or *Gomphonema* species were often volumetrically important. Of the more than 25 species of *Navicula* identified, only *Navicula accomoda* Hust. occurred more than 5 percent of the time in yearly average data, although several *Navicula* species were common in individual samples (Table III). Most of the 24 Surirellinees species were large forms, and often volumetrically abundant. Species such as *Epithemia sorex* Kütz. and some of the *Nitzschia* species were also numerically important. In the following sections abundancies of all the *Nitzschia* species are combined, because of the similar water quality tolerances of all species in the genus (Hancock, 1973) and the difficulty and uncertainty involved in identifying the individual *Nitzschia* species.

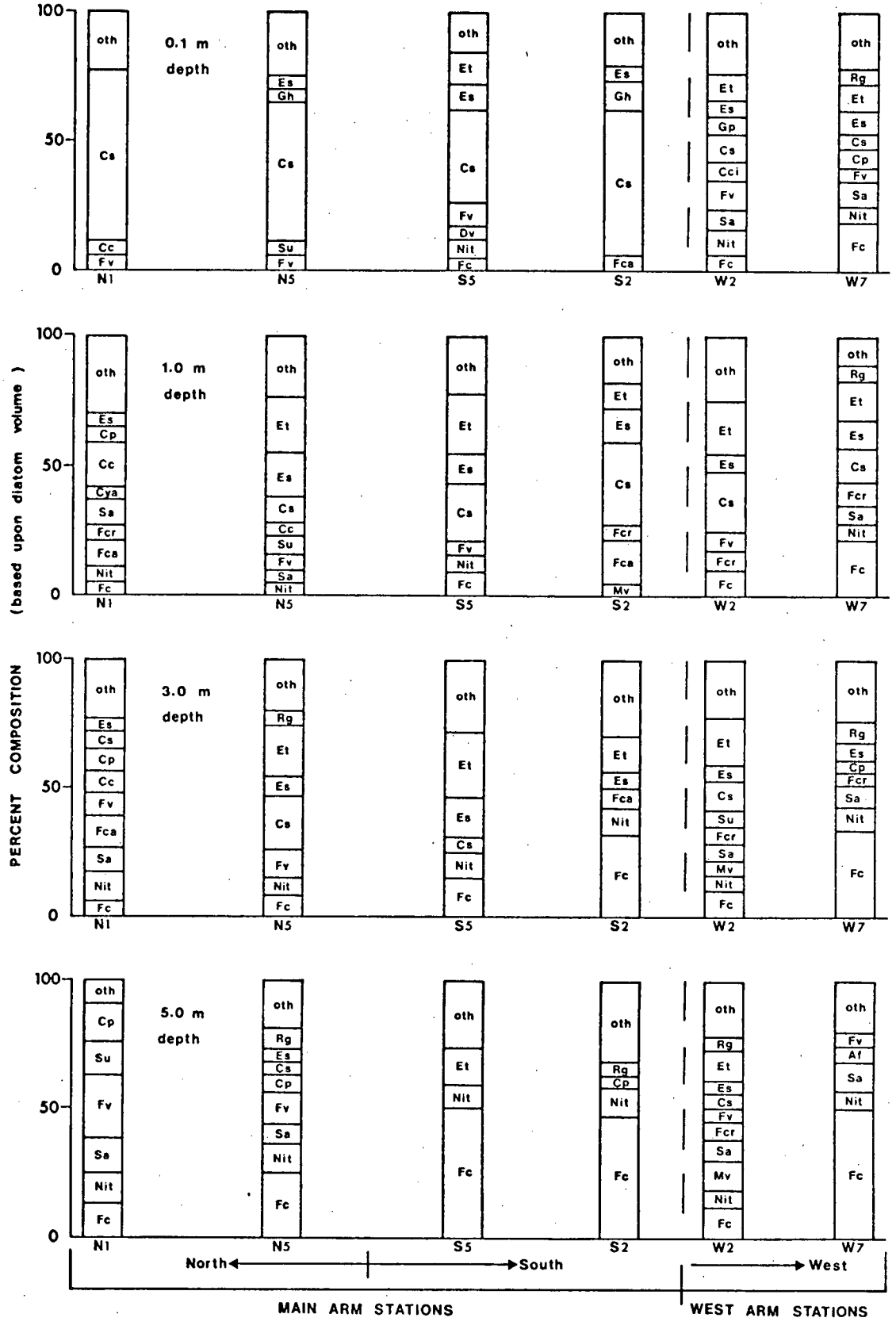
i. Natural Substrates

Most of the 24 diatom species that were considered numerically and/or volumetrically important (on natural substrates over the course of the year) occurred at all stations, but in varying amounts. However, only a few species were common (accounted for 5 percent or more of the averaged samples) at all stations. *Achnanthes minutissima* exhibited such a trend in the numerical

Fig. 47. Average percent numeric composition of common diatom species (≥ 5 percent of the total number) attached to natural rock substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. The species are: Af, *Asterionella formosa;* Am, *Achnanthes minutissima;* Aop, *Amphora ovalis* v. *pediculus;* Cc, *Cymbella caespitosa;* Cv, *Cymbella ventricosa;* Es, *Epithemia sorex;* Fc, *Fragilaria construens* complex; Fca, *Fragilaria capucina;* Fcr, *Fragilaria crotonensis;* Fv, *Fragilaria vaucheriae;* Gp, *Gomphonema parvulum;* Nit, *Nitzschia* species complex; Oth, all other species; Sam, *Stephanodiscus astraea* v. *minutula.*


PERCENT COMPOSITION (based upon diatom numbers)
100
50
0
0.1 m depth
1.0 m depth
3.0 m depth
5.0 m depth
oth
Es
Cc
Fv
Fcr
Fca
Am
Nit
Fc
Cv
Aop
Gp
Af
Sam
N1
N5
S5
S2
W2
W7
North
South
West
MAIN LAKE STATIONS
WEST ARM STATIONS

Fig. 48. Average percent volumetric composition of common diatom species (≥ 5 percent of the total volume) attached to natural rock substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. The species are: Af, *Asterionella formosa;* Cc, *Cymbella caespitosa;* Cci, *Cymbella cistula;* Cs, *Cymbella* sp. "A"; Cp, *Cymbella prostrata;* Cya, *Cymbella aspera;* Dv, *Diatoma vulgare;* Es, *Epithemia sorex;* Et, *Epithemia turgida;* Fc, *Fragilaria construens* complex; Fca, *Fragilaria capucina;* Fcr, *Fragilaria crotonensis;* Fv, *Fragilaria vaucheriae;* Gh, *Gomphonema herculeanum;* Gp, *Gomphonema parvulum;* Mv, *Melosira varians;* Nit, *Nitzschia* species complex; Oth, all other species; Rg, *Rhopalodia gibba;* Sa, *Stephanodiscus astraea;* Su, *Synedra ulna.*


0.1 m depth
1.0 m depth
3.0 m depth
5.0 m depth
PERCENT COMPOSITION (based upon diatom volume)
100
50
0
N1
N5
S5
S2
W2
W7
North
South
West
MAIN ARM STATIONS
WEST ARM STATIONS

analysis (Fig. 47), although this small species was not volumetrically abundant (Fig. 48). The *Nitzschia* species complex was also widespread, both in terms of cell numbers and cell volumes. *Epithemia sorex* contributed greatly to the diatom volume at all stations. *Cymbella* sp. "A", a relatively large species was volumetrically important near the lake surface at all locations.

There were definite distributional patterns related to the depth at which the diatoms were collected. As mentioned previously, species near the main lake surface were larger (and had gelatinous sheaths or stalks). In the protected west arm of the lake, however, the surface flora more closely resembled the diatoms at deeper depths (Fig. 47, 48). *Gomphonema herculeanum* Ehr. and *Cymbella* sp. "A" are representative diatoms from the splash zone of the main lake.

Some species were restricted to, or more common in, specific regions of Kootenay Lake. *Epithemia turgida* (Ehr.) Kütz., important in terms of cell volume, was generally more common in the south end of the lake (Fig. 48). *Fragilaria construens* and varities clearly increased in abundance southwards and westwards in the lake (Fig. 47, 48). The *F. construens* complex also increased in abundance with depth; at the 5.0 m depth in the south arm of the lake it accounted for 75 percent of the diatom numbers and about 50 percent of the diatom volume. No other species consistently dominated the diatom flora as did *F. construens*, and few species exhibited such distinct distributional gradients.

Fragilaria vaucheriae (Kütz.) Peters., *Cymbella caespitosa* (Kütz.) Brun, *Cymbella prostrata* (Berk.) Cl. and *Synedra ulna* (Nitz.) Ehr. tended to

be more abundant in the north arm of Kootenay Lake (Fig. 47, 48).

Asterionella formosa Hass., *Fragilaria crotonensis* Kitton, *Melosira varians* Ag. and *Stephanodiscus astraea* (Ehr.) Grun. were most common in the west arm (Fig. 47, 48). It is interesting to note that this entire species group is generally considered planktonic. Their greater abundance in the river-lake west arm may be a result of planktonic species settling out of water which originates from the more lentic parts of the lake.

Most of the species enumerated were only occasionally common or else had disjointed distributions, apparently unrelated to lake location. In the numerical analysis, *Stephanodiscus astraea* v. *minutula* (Kütz.) Grun., *Fragilaria capucina* Desm., *F. crotonensis*, *Amphora ovalis* v. *pediculus* (Kütz.) Van Heurck, *Cymbella ventricosa* Kütz., *Gomphonema parvulum* (Kütz.) Kütz., and *Epithemia sorex* Kütz., all illustrate this distributional pattern. In the volumetric analysis, *Diatoma vulgare* Bory, *F. capucina*, *Cymbella aspera* (Ehr.) Cl., *G. parvulum* and *Rhopalodia gibba* (Ehr.) O. Müll. were occasionally common and had spotty distributions.

In addition to a consideration of individual species distributions, a comparison of the average number of common species in various regions of the lake is useful. A large number of common species at a station would represent diverse conditions, while fewer species at a station would represent less diverse conditions (where fewer species form a major proportion of the community biomass). In Kootenay Lake, the north arm supports more common species than does the south arm. Numerically, there are an average of 5.9 common species at the north arm stations while the south arm has only 4.6 common species per station. Volumetrically, there are an average of 6.9

common species in the north arm and only 5.0 common species in the south arm.

ii. Artificial Substrates

Diatom distributional patterns on artificial substrates (Fig. 49, 50) were similar to patterns observed on the natural substrates. All but one of the 24 species that were common (over the year) on natural substrates were also common the artificial substrates. Although there were more common species on the artificial substrates (32 versus 24) the additional species were only occasionally abundant and had spotty or single common occurrences.

As observed for natural populations, few species on artificial substrates were widespread or abundant in all the arms of Kootenay Lake. Also, species which had distinct patterns of occurrence on the natural substrates exhibited the same distribution (with only a few exceptions) on the artificial substrates. Furthermore, most species on artificial substrates were only occasionally common or else had disjointed occurrences that could not be related to major lake regions.

Although diatom species trends were similar on the two types of substrate, actual levels of abundance were seldom identical. Most common species, particularly *Achnanthes minutissima* and the *Fragilaria construens* complex, were not as abundant on the artificial substrates. The more even distribution of species numbers could perhaps be related to the short two-week exposure period which should reduce the amount of diatom competition on the artificial substrates. Not surprisingly, there are, on a yearly average, more common diatoms per sample on the artificial substrates than on the

Fig. 49. Average percent numeric composition of common diatom species (≥ 5 percent of the total number) attached to artificial substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. The species are: AF, *Asterionella formosa;* Am, *Achnanthes minutissima;* Aop, *Amphora ovalis* v. *pediculus;* Cc, *Cymbella caespitosa;* Cci, *Cymbella cistula;* Cv, *Cymbella ventricosa;* Cyg, *Cyclotella glomerata;* Dt, *Diatoma tenue;* Es, *Epithemia sorex;* Fc, *Fragilaria construens* complex; Fca, *Fragilaria capucina;* Fcr, *Fragilaria crotonensis;* Fv, *Fragilaria vaucheriae;* Gh, *Gomphonema herculeanum;* Gms, *Gomphonema montanum* v. *subclavatum;* Na, *Navicula accomoda;* Nit, *Nitzschia* species complex; Oth, all other species; Sa, *Stephanodiscus astraea;* Sam, *Stephanodiscus astraea* v. *minutula;* Sh, *Stephanodiscus hantzschii;* Sm, *Synedra mazamaensis;* Ss, *Synedra acus.*

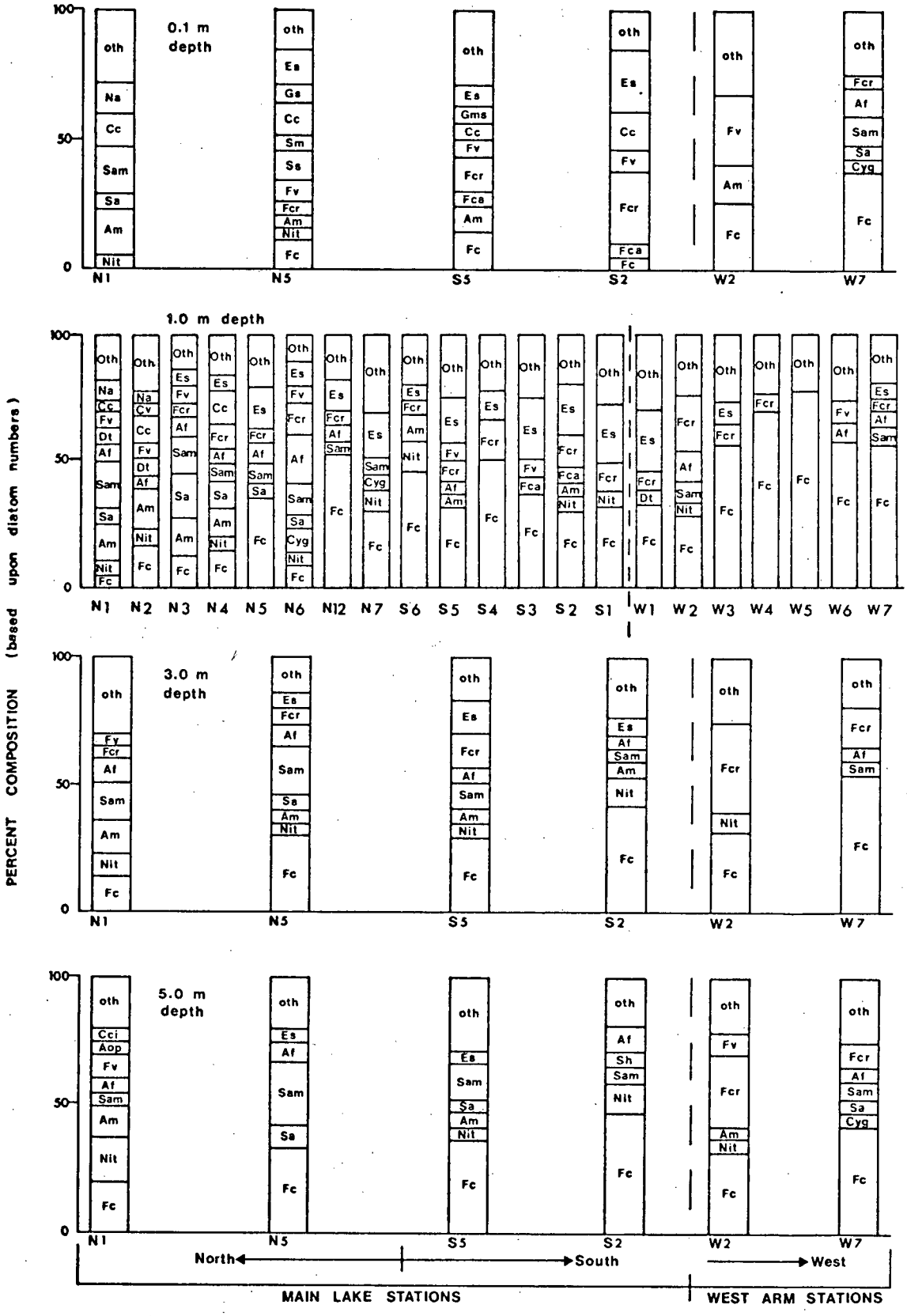
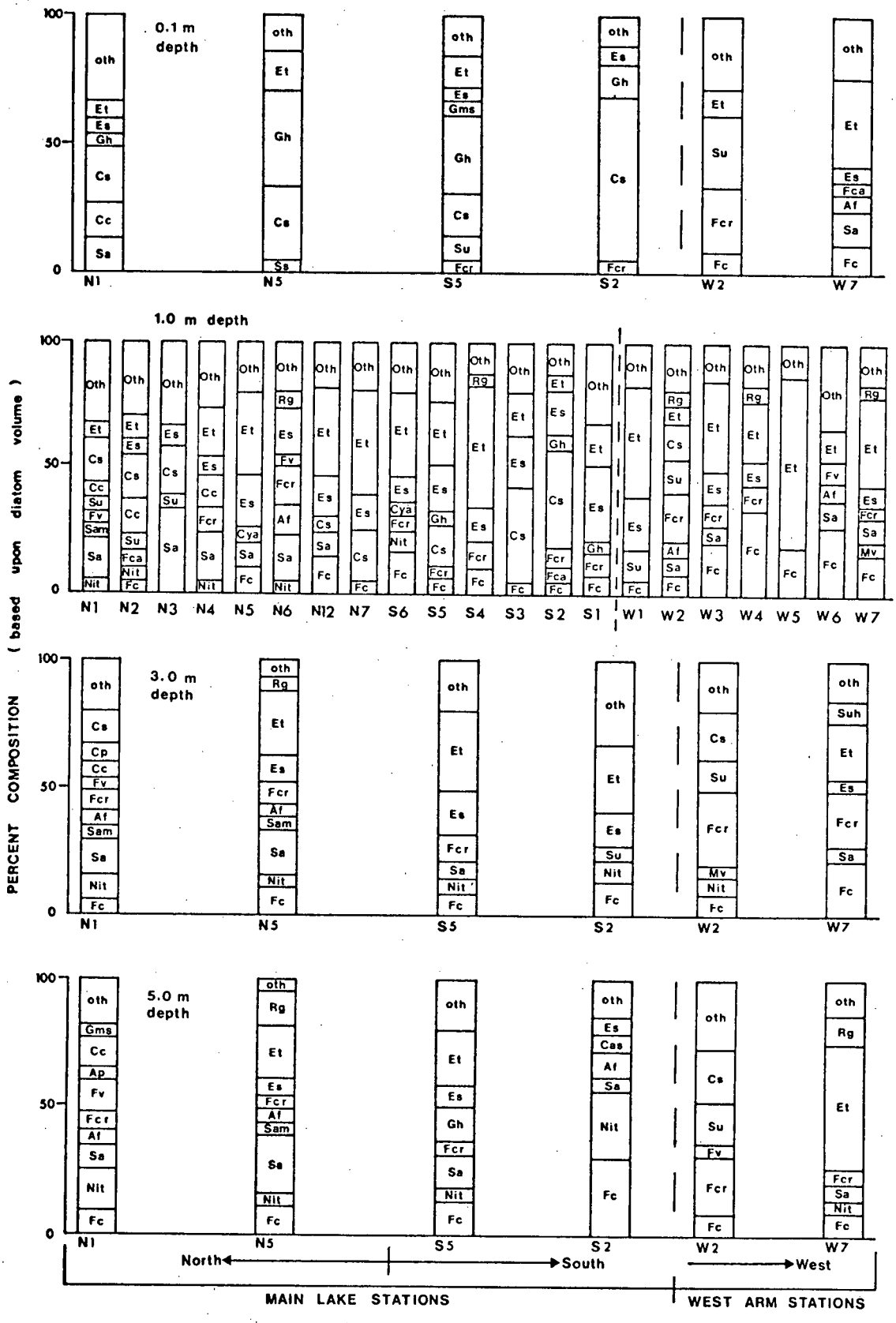

0.1 m depth
1.0 m depth
3.0 m depth
5.0 m depth
PERCENT COMPOSITION (based upon diatom numbers)
100
50
0
N1 N2 N3 N4 N5 N6 N12 N7 S6 S5 S4 S3 S2 S1 W1 W2 W3 W4 W5 W6 W7
North
South
West
MAIN LAKE STATIONS
WEST ARM STATIONS

Fig. 50. Average percent volumetric composition of common diatom species (≥ 5 percent of the total volume) attached to artificial substrates at 0.1, 1.0, 3.0, and 5.0 m in Kootenay Lake, 1973. The species are: AF, *Asterionella formosa;* Ap, *Amphipleura pellucida;* Cas, *Caloneis* sp.; Cc, *Cymbella caespitosa;* Cs, *Cymbella* sp. "A"; Cp, *Cymbella prostrata;* Cya, *Cymbella aspera;* Es, *Epithemia sorex;* Et, *Epithemia turgida;* Fc, *Fragilaria construens* complex; Fca, *Fragilaria capucina;* Fcr, *Fragilaria crotonensis;* Fv, *Fragilaria vaucheriae;* Gh, *Gomphonema herculeanum;* Gms, *Gomphonema montanum* v. *subclavatum;* Mv, *Melosira varians;* Nit, *Nitzschia* species complex Oth, all other species; Rg, *Rhopalodia gibba;* Sa, *Stephanodiscus astraea;* Sam, *Stephanodiscus astraea* v. *minutula;* Ss, *Synedra acus;* Su, *Synedra ulna;* Suh, *Surirella helvetica.*


0.1 m depth
1.0 m depth
3.0 m depth
5.0 m depth
PERCENT COMPOSITION (based upon diatom volume)
100
50
0
N1
N2
N3
N4
N5
N6
N12
N7
S6
S5
S4
S3
S2
S1
W1
W2
W3
W4
W5
W6
W7
North
South
West
MAIN LAKE STATIONS
WEST ARM STATIONS

natural substrates (and, as mentioned previously, more individual common species--32 versus 24). However, trends in lakewide distributions of common species on the two types of substrates were similar, with more common species in the north arm than in the south arm of Kootenay Lake. Numerically, there were 7.5 common species in the north arm and only 5.5 common species in the south arm, on artificial substrates. Similarly, in the volumetric analysis there were 6.7 common species in the north arm and 5.7 common species in the south arm.

Transfer Experiments

Reciprocal transfer experiment results are summarized for the diatoms *Fragilaria construens* plus varieties (Fig. 51) and for *F. vaucheriae* (Fig. 52). These two morphologically similar species were chosen as diatom distribution data indicated that they represent opposite extremes in their type of distribution. *Fragilaria construens* is more common in the eutrophic southern and westerm extremities of the lake, while *F. vaucheriae* is common in the more oligotrophic north arm. The reciprocal transfers involving these two species were designed to provide additional data on the relative importance of water chemistry in determining their distributional patterns.

At the time the algal substrates were transferred from the original sites (see methods for a complete description of the procedure), the abundances of the diatom species were supposedly the same at all stations. This initial abundance is represented by the dashed horizontal lines in figures 51 and 52. Since little additional production should occur on these plates which were already colonized for two weeks (Patrick et al., 1954), any

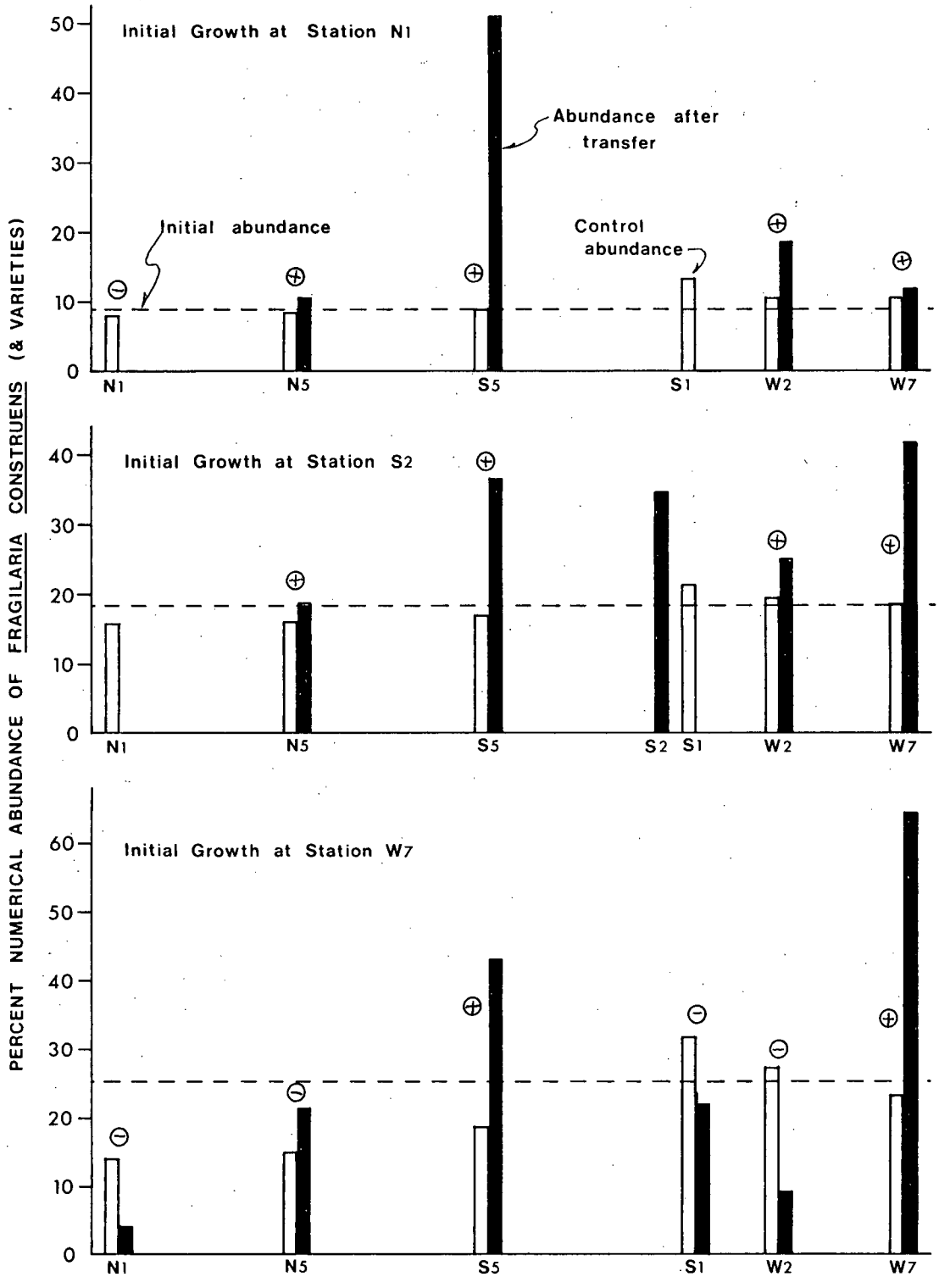


Fig. 51. Growth response of the diatom *Fragilaria construens* after the reciprocal transfer experiments at 1.0 m in Kootenay Lake; 21 May-17 June, 1973. Dashed horizontal lines indicate initial abundances, open rectangles are control abundances, solid rectangles are transfer abundances, positive symbols represent successful competition, negative symbols represent unsuccessful competition. Missing values are the result of lost artificial substrates.

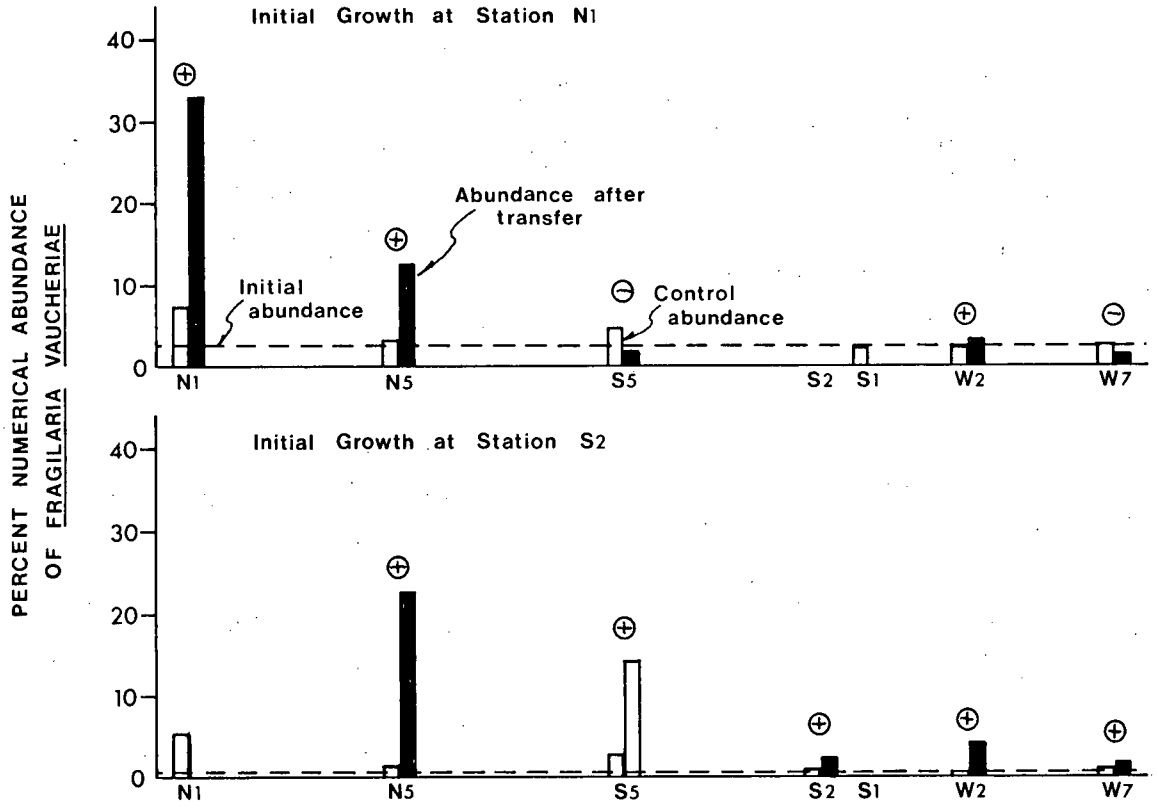


Fig. 52. Growth response of the diatom *Fragilaria vaucheriae* after the reciprocal transfer experiments at 1.0 m in Kootenay Lake; 21 May-17 June, 1973. Dashed horizontal lines indicate initial abundances, open rectangles are control abundances, solid rectangles are transfer abundances, positive symbols represent successful competition, negative symbols represent unsuccessful competition. Missing values are the result of lost artificial substrates.

increases or decreases in a species' relative abundance should primarily be a result of competition as influenced by factors such as water chemistry. Nevertheless, uncolonized control substrates (open rectangles, Fig. 51 and 52) were immersed at the time of the transfer to measure diatom production and settling rates. Since results are plotted in terms of percentage abundance rather than actual numbers, local settling rates could only alter a species abundance when control percentage abundances are greater than transfer percentage abundances (solid rectangles, Fig. 51 and 52).

Fragilaria construens, whether initially grown in the north, south or west arm showed negative competitive responses or else very minor positive responses when transferred to the north arm of the lake (Fig. 51). (Missing values are the result of lost artificial substrates.) When transferred to the south arm, *F. construens* markedly increased its percentage numerical abundance, except for one slightly negative response. Results for populations transferred to the west arm are comparable to south arm responses. Evidently this species, which is most abundant in the eutrophic areas of the lake, is generally competitively successful in those areas when compared to the other species. When transferred to the more oligotrophic regions, *F. construens* loses its competitive advantage and its percentage numerical abundance decreases slightly.

Fragilaria vaucheriae, most abundant in the north arm of the lake, greatly increased its percentage abundance when transferred to the north arm of the lake (Fig. 52). Responses in the south arm are less clear, for it twice increased in abundance and once decreased. Results also indicated only slight positive or negative responses when *F. vaucheriae* was grown in the lake's west arm. (Initial growth of *F. vaucheriae* in the west arm was

below detection limits so that transfer results are only presented for populations initially grown in the north or south arms of the lake.)

DISCUSSION

Since 1953, when a Cominco Ltd. fertilizer plant began operations, increased phosphate loadings to Kootenay Lake have affected the lake's limnology. Chemical data from this and other studies (Davis, MS 1973; Northcote 1972b, 1973a) have confirmed that phosphorus concentrations within the lake have increased in response to the increased loadings. Prior to the fertilizer plant development, dissolved orthophosphate concentrations in 1949/1950 were about 0.001 mg l^{-1} (Northcote, 1973a), placing Kootenay Lake in the oligotrophic category. In response to pollution loads of as much as 8000 metric tons of phosphorus per year, dissolved orthophosphate concentrations within the lake are now usually over 0.05 mg l^{-1} during spring freshet. The phosphate concentrations are sometimes as high as 0.18 mg l^{-1} and, as values over 0.01 mg l^{-1} often cause algal problems (Vollenweider, 1971; Dillon and Rigler, 1975), the lake can now be described as eutrophic.

Since most of the natural background phosphorus and virtually all the industrial pollution phosphorus enters the southern extremity of the lake (Northcote, 1973a - Fig. 5) via the Kootenay River inlet, a phosphate gradient would be expected within Kootenay Lake. Theoretically, the south arm should have high levels; the north arm, fed by the nutrient poor Duncan River, should have low levels; and the west arm outlet, which receives water from the south and north basins, should have intermediate phosphorus levels. Loadings of most other materials are also highest at the south end of the lake and the distributions of conservative elements such as total dissolved solids, calcium and sodium do conform to the expected gradient (Fig. 17,

21, 22). Surprisingly, however, there appears to be little measurable variation in the lake's phosphorus content (Fig. 13, 15).

But phosphorus is rapidly utilized by algae and this biological utilization often creates differences between expected and observed phosphorus concentrations. To minimize the effects of phosphorus uptake by algae, Vollenweider (1971), Edmondson (1972), Dillon and Rigler (1974, 1975) and others use late winter or spring maximum phosphorus values in determining a lake's trophic state and in predicting the planktonic algal biomass during the next summer. But in Kootenay Lake, even early spring phosphorus values (Fig. 13) showed little regional variation, compared to the expected phosphorus gradient based upon the vast differences in loadings to the north and south extremities of the lake (Fig. 12). The relationship between early spring phosphate levels and planktonic algal biomass, while accounting for phosphate uptake by planktonic algae, do assume that early spring algal populations are low and of minimal importance. In Kootenay Lake, attached algal populations did not decrease dramatically during winter (Fig. 29). It is therefore not surprising that, even during early spring, inshore phosphorus readings in Kootenay Lake do not exhibit the expected regional variations.

Phosphorus incorporation by Kootenay Lake's attached algae was determined indirectly, by multiplying daily growth rates by the amount of phosphorus normally occurring in algal cells. At station W1, for instance, maximum growth rates reached 0.32 mg organic cm^{-2} day^{-1} or 1.423 mg dry weight cm^{-2} day^{-1} (using an empirically derived conversion for Kootenay Lake attached algae of 1 mg organic: 4.45 mg dry weight). Assuming an average algal phosphorus content of 11 μg mg^{-1} (Healey, 1973), phosphorus

incorporation during the day would be near 15.65 µg P cm^{-2} or up to 46.96 µg P cm^{-2} for cells rich in phosphorus (phosphorus content can reach 33 µg mg^{-1} algae; Healey, 1973). Phosphate incorporations this high in growing algae (not considering luxury uptake by algae already present) would reduce the phosphorus content of the water near the attached algae, and could conceivably mask any phosphorus gradient within Kootenay Lake.

The amount of surplus stored phosphorus in the algal cells was measured, and resultant data indicate that attached algal phosphorus utilization and storage are high (Fig. 30, top). Furthermore, the regional variation in the algal phosphorus storage corresponds well with the lake's expected phosphorus gradient, south arm phosphorus storage being greater than north arm storage. The amounts of phosphorus storage in the south arm were always indicative of eutrophic conditions (Fitzgerald, 1969). But a maximum level of about 2.5 µg mg^{-1} dry weight algae at station S5 was not excessively high. Lin (1971) reported values as high as 8.4 µg from *Cladophora* populations, and Fitzgerald (1969) noted that during a planktonic blue-green algal bloom in eutrophic Lake Mendota phosphorus storage reached levels of 4.2 µg mg^{-1} dry weight algae. Data from the north and west arms of Kootenay Lake are often, but not always, typical of phosphorus limited algal populations. Some readings from station N5, for instance, were as high as 1.5 µg, while several other readings in the north arm were below 1 µg, indicative of phosphorus limited populations (Fitzgerald, 1969).

The amount of surplus stored phosphorus per unit area of rock surface (rather than per dry weight of algae) also shows that there is more phosphorus storage in the south arm of the lake (Fig. 30, bottom). Differences

in algal abundance per unit area did not significantly affect the surplus phosphorus storage results, and the argument that less algae in one lake region enables more phosphorus to be stored per unit weight of algae is not valid.

Algal populations are influenced by many physical factors which must be accounted for, as these variables can potentially complicate or negate the attached algal responses to nutrient conditions alone. Physical factors such as turbulence, lake level fluctuations, temperature and light energy were measured, when practicable, and a stepwise multiple regression analysis was performed using these variables and chemical data, to assess the relative importance of each factor. Unfortunately, the variables alone, or in combination, seldom accounted for much of the variability in algal abundance, production or species composition. Furthermore, factors which were most important in explaining some aspect of algal variability, say abundance, were seldom as important in explaining other aspects of the algal variability, such as the amount of green algae present. Probable shortcomings which could explain the inability of the multiple regression analyses to account for differences in algal populations include: the masking of chemical conditions by biological utilization and luxury consumption, the difficulty in quantifying physical factors such as lake level fluctuations, lack of data on lake turbulence and grazing rates, and the difficulty in assessing the short term history of several parameters on the algal community.

However, the sampling program, whereby algal collections were made at several depths, does allow a qualitative measure of the relative importance of various physical variables compared to chemical variables in regulating Kootenay Lake's attached algae. Near the lake surface, for instance,

regional differences in light penetration would be of minimal importance, whereas the amount of lake turbulence (1.0 m waves frequently occurred) and degree of water level fluctuations (up to 1.3 m per week, Fig. 5) could possibly override any algal responses to nutrient variations. Similarly, at the deeper depths differences in light penetration could complicate the algal response to chemical differences, but other physical factors such as lake turbulence would have little effect.

Chlorophyll a content near the lake surface (Fig. 23) was generally low, but conditions were extremely variable. During stable water level periods, the highest chlorophyll levels of the study occurred at the 0.1 m depth. This extreme variability, combined with a lack of regional variation, indicates that physical factors such as lake turbulence and water level fluctuations are more important than chemical conditions in regulating algal populations near the lake surface. The general increase in chlorophyll content with depth is indicative of a more physically benign environment. Despite the lower light penetration in the south arm of the lake (Fig. 9) chlorophyll is highest there, indicating the major importance of regional phosphorus variations and the minor effect of physical factors in regulating the algal abundance.

Chlorophyll a content averaging 7 $\mu g\ cm^{-2}$ in Kootenay Lake's south arm is indicative of eutrophic conditions, while north arm readings are lower and indicative of more oligotrophic conditions (Fig. 23, 24). Kootenay Lake and lakes from the Okanagan Valley of British Columbia both drain into the Columbia River, and both lake systems show similar attached algal responses to eutrophication. Chlorophyll content in Kootenay Lake's south arm is comparable to levels found in Wood Lake, Skaha Lake and

Osoyoos Lake which also suffer from over-enrichment (Stockner, Pomeroy, Carney, and Findlay; MS 1972). Kootenay Lake's north arm has chlorophyll levels that resemble those from Kalamalka Lake--the most oligotrophic of the Okanagan chain (Stockner et al., MS 1972). These north arm values are also similar to levels found at Stony Point Bay in oligotrophic Lake Superior (Stokes, Olson, and Odlaug; 1970), where mean chlorophyll a content ranged from 1.49 - 7.35 µg cm $^{-2}$. However, north arm values are certainly much higher than in ultra oligotrophic systems such as Carnation Creek on Vancouver Island, where chlorophyll a values in non-estuary regions average only 0.19 µg cm $^{-2}$ (Stockner and Shortreed, 1975).

Vertical variations in organic weight paralleled chlorophyll a patterns. However, regional variations in the amount of organics only occurred during summer months (Fig. 27) when phosphorus concentrations were lowest. At that time, south arm organic weights were higher than north arm organic weights. Summer organic weights in the south arm of the lake (Fig. 27) were similar to maximum values of 2 - 3 mg organic cm $^{-2}$ reported from the more eutrophic lakes in the Okanagan Valley (Stockner et al., MS 1972). Biomasses were also equal to or greater than attached algal weight in other eutrophic systems such as the Ohio River near Cincinnati where weights were less than 1 mg cm $^{-1}$ (Weber and Raschke, 1970), Sedlice Reservoir in Czechoslovakia where weight ranged from 0 - 4.91 mg cm $^{-2}$ (Sládeček and Sládečková, 1964) and the productive Ohanapecosh Hot Springs in Washington State where accumulations only reached 0.764 mg cm $^{-2}$ (Stockner, 1968). But, south arm values were not excessively high, and were certainly less than values of 7.3 mg cm $^{-2}$ reported from eutrophic Lake Tiberias in Israel (Dor, 1970).

Summer organic weights from the north arm of the lake (Fig. 27) were usually under 2 mg cm $^{-2}$ at the deeper depths, and under 1 mg cm $^{-2}$ at the shallow depths. Although these weights were similar to some in surprisingly low biomass eutrophic waters, they were more typical of oligotrophic systems. Kalamalka Lake in the Okanagan, for instance, had weights of about 1.0 mg cm $^{-2}$ (Stockner et al., MS 1972), Lake Superior's periphyton averaged between 0.91 - 1.7 mg organic cm $^{-2}$ (Fox et al., 1969) and a maximum reading in unfertilized Lake 240 of the Experimental Lakes Area in northwestern Ontario was only 1.25 mg organic cm $^{-2}$ (Stockner and Armstrong, 1971). But, values were much greater than in ultra oligotrophic Carnation Creek on Vancouver Island, where average crops only reached 0.086 mg cm $^{-2}$ in non-estuary regions (Stockner and Shortreed, 1975). Furthermore, organic weights in the north arm during non-summer periods, when phosphorus readings were higher, resembled south arm weights and were typical of weights in many eutrophic waters.

Estimates of net primary production rates in this study are, at best, crude approximations of true production rates within Kootenay Lake, and results must be interpreted with care. The absence of *Cladophora aegagropila*, an important component of the natural attached algal assemblage at the deeper depths in the lake's south arm, combined with the greater abundance of most other green algal species on the artificial production substrates, surely results in some errors in estimation of production rates. At the beginning of the incubation period, the bare artificial substrates present an excellent habitat for attached algal growth in the normally crowded and space-limited littoral zone. These potential production rates

no doubt exceed actual production rates on the space-limited natural surfaces, a problem inherent in the method used but not encountered in studies using C^{14} and oxygen light-dark productivity methods. Comparisons with production rates determined by these other methods are also difficult because the artificial method is subject to natural regulating factors such as grazing, peeling and sloughing-off while C^{14} and oxygen light-dark techniques largely avoid these complications.

Kootenay Lake's attached algal production rates at the 0.1 and 1.0 m depths reflected the regional differences in phosphorus loadings, with highest production rates occurring at the lake's south end and decreasing northwards and westwards (Fig. 31). Regional variations did not occur at the deeper depths but, as mentioned, *Cladophora aegagropila* did not grow on the artificial production substrates as it did on natural rock surfaces in the lake's south end. If *C. aegrogropila* had grown on the artificial substrates, production rates at the deep depths would certainly have been greatest in the south arm as observed at the shallow depths.

Interestingly, production rates exhibited opposite depthwise trends to algal biomass, with highest production rates at the shallow depths and lowest rates at the 3.0 and 5.0 m depths (even in the lake's north arm where *C. aegagropila* never occurred and could not bias the comparisons). This high algal production rate at the shallow depths (Fig. 31) contrasted with the low biomasses actually occurring there (Fig. 23, 25) suggests that factors other than water quality influence surface algal populations. Furthermore, since surface algal biomasses were approximately the same throughout the lake despite the higher production capabilities in the more eutrophic regions, it appears that those other factors (probably changing lake levels and

turbulence) are most important and completely mask most algal responses to water chemistry at shallow depths. Conversely, the lower production rates at 3.0 and 5.0 m (probably because of light limitations--especially in the lake's south arm) contrasted with the greater biomasses occurring there suggests that these depths are generally benign. These algal populations (with slower growths and higher biomasses than at the shallow depths) are probably older and more likely to be affected by differences in water chemistry. The occurrence of greater biomasses in the more nutrient rich south arm, despite the lower light levels there, attests to the importance of water chemistry in influencing those populations.

Daily production rates at the 0.1 and 1.0 m depths of about 0.02 - 0.03 mg organic cm $^{-2}$ in the south arm (Fig. 31) are similar to values reported from other eutrophic waters. {Data from other studies have often been transformed to express production in terms of units used in this study. Mg of carbon produced were multiplied by 0.43 (average percent carbon in dry weight algal cells--Healey, 1973) and then divided by 4.4 (average dry weight/organic weight ratio in Kootenay Lake's attached algae). Production in terms of dry weight was likewise divided by 4.4 to express it in terms of organic weight.} Daily production in eutrophic Lake Tiberias in Israel, for instance, ranges from .0027 - .0436 mg organic cm $^{-2}$ (Dor, 1970). Daily production rates expressed in terms of my organic cm $^{-2}$ in other eutrophic waters follow: Sedlice Reservoir in Czechoslovakia has a mean net production rate of 0.0174 (Sládeček and Sládečková, 1964), Danish Lake Furesøhas a rate of 0.0426 (Hunding, 1971), Borax Lake a rate of 0.038 (Wetzel, 1963), thermal stream Ohanapecosh in Washington State a rate of 0.0005 - 0.05 (Stockner, 1968), and

Red Cedar River in Michigan a rate of 0.0281 (King and Ball, 1966). Production rates in all lakes from the Okanagan Valley (Stockner et al., MS 1972) were above 0.01 mg organic cm $^{-2}$, and similar to rates in the south arm of Kootenay Lake.

Although production rates in even the oligotrophic Okanagan Lakes were high, most other oligotrophic systems had amazingly low rates. Compared to those systems, production rates of about 0.008 mg organic cm $^{-2}$ in the surface waters of Kootenay Lake's north arm and at the deeper depths (0.005 - 0.01 mg organic cm $^{-2}$) throughout the lake could best be described as typical of mesotrophic systems. Rates in Lake Superior, for instance, ranged from 6.0 to 9.0 x 10 $^{-6}$ mg organic cm $^{-2}$ (Fox et al., 1969). Carnation and Ritherdon Creeks on Vancouver Island had rates of 0.004-0.006 mg organic cm $^{-2}$ (Stockner and Shortreed, 1975) while Jacobs (Marion) Lake near Haney, B.C. had an attached algal production rate of 0.0057 mg organic cm $^{-2}$ (Hargrave, 1969).

The attached algal assemblage in Kootenay Lake is similar in some respects to attached assemblages in other north temperate lakes, with diatoms, greens and blue-greens being the only important algal groups. However, diatoms are more abundant in this lake than in other North American lakes (Evans and Stockner, 1972; Fox et al., 1969; Stockner and Armstrong, 1971). The great abundance of diatoms in Kootenay Lake does not preclude the possibility that this lake could be eutrophic, since nutrient rich waters can be dominated by certain diatom species as well as by green or blue-green algae. Furthermore, in Kootenay Lake green algae sometimes dominate for short periods, especially during the spring and fall (Fig. 33) when distinct

bands of green algae occur near the lake surface.

Despite the general diatom dominance, there were some distinct gradients and variations in the abundance of the major algal classes within Kootenay Lake. Blue-green algae generally increased along the length of the west arm (Fig. 32). Several blue-green species, such as *Calothrix* sp., *Phormidium* sp., *Sacconema rupestre* and *Tolypothrix distorta*, were also localized in that region of the lake. It is well known that this algal group often increases with sewage pollution where nitrates, phosphates and concentrations of organics are increased. The high nitrate and phoshpate loadings (Northcote, 1972b) in the heavily populated west arm do indicate the probable existence of sewage pollution and thus explain increases in blue-green algae there. In contrast, the main lake has only high inorganic (fertilizer plant) phosphate loadings, and smaller populations of blue-green algae occur there.

At the deeper depths, the increase in green algae at the south end of the lake is attributable to the occurrence of *Cladophora aegagropila* (Fig. 35 top, 36). This alga is a shade-loving species which seems to occur only in eutrophic waters such as the Seine River at Paris (Hoek, 1963). Its absence in the north arm can be attributed to lack of nutrients but not to subsurface illumination, as *C. aegagropila* was absent at even the 10.0 and 14.0 m depth where light levels are even less than those at the 3.0 and 5.0 m depths in the south arm. Other *Cladophora* species also appear to be indicative of waters rich in nutrients, particularly phosphorus. Pitcairn and Hawkes (1973) found that in a number of English rivers the standing crop of *Cladophora* was correlated with phosphorus concentrations. Adams and Stone

(1973) found that *Cladophora* photosynthesis was correlated with phosphorus in Lake Michigan. Also in Lake Michigan, Lin (1971) noted that *Cladophora glomerata* biomasses increased near phosphorus sources and that the amount of excess stored phosphorus in the alga also increased. *Cladophora* was also reported from a number of other eutrophic lakes and rivers including Lake Ontario (Bellis and McLarty, 1967), the lower Fraser River (Northcote et al., 1975) and several lakes in the Okanagan Valley (Stockner et al., MS 1972). In Kootenay Lake, *Cladophora* populations were also highest during the warmest months, as Verduin (1972) observed in the Laurentian Great Lakes. During peak growing periods, Whitton (1970) found that *C. glomerata* could double its fresh weight in 21-26 hours. Such data confirm that *Cladophora* is simply unable to grow on artificial substrates, not that the two week exposure period was too short a time to grow the species, as Hynes (1960) suggests can be the case for some species, especially encrusting forms. It is also interesting to note that Kootenay Lake's *Cladophora* was extensively covered with epiphytes, a condition which is rare for nitrogen limited populations (Whitton, 1971). Apparently, there is enough background nitrogen loading to the lake to support the large algal biomasses responding to the increased phosphorus loads.

The increase in diatom numbers with depth (Fig. 37) corresponds to the organic weight and chlorophyll a pattern. Also, the higher diatom production rate (Fig. 39) nearer the lake surface agrees well with other biomass results. Both types of data support the contention that attached algae at 3.0 and 5.0 m are more influenced by the water quality than are fast growing but more exposed and therefore less abundant surface populations.

The length of exposure probably influences the numbers of diatoms and other types of algae produced on artificial glass or plexiglas substrates. In Kootenay Lake diatom numbers are higher on natural substrates than on artificial substrates. Obviously, diatom numbers obtained from artificial glass or plexiglas substrates immersed for varying amounts of time cannot be easily compared unless exposure periods are similar. In particular, Butcher's (1949) trophic classification of rivers, based upon diatom numbers attached to glass slides (in his case for 20-30 day periods; Butcher, 1940) must be considered invalid because of the effect of the exposure period. Butcher states that oligotrophic rivers support diatom numbers ranging from 0.1×10^6 - 0.5×10^6 cells cm $^{-2}$ and natural eutrophic rivers have populations of 0.5×10^6 - 1.0×10^6 cells cm $^{-2}$. These supposedly high diatom numbers obtained from the artificial substrates, are in fact much less than diatom numbers obtained from natural substrates in both oligotrophic and eutrophic lakes and rivers (Fox et al., 1969; Northcote et al., 1975; Tai and Hodgkiss, 1975).

Numerical diatom density in Kootenay Lake (ranging from 0.5×10^6 - 3.5×10^6 cells cm $^{-2}$) agrees well with many recent investigations where natural assemblages were studied. Results are similar to values ranging from $.497 \times 10^6$ - 1.47×10^6 cells cm $^{-2}$ reported from oligotrophic Lake Superior (Fox et al., 1969) and much less than 1.98×10^7 cells cm $^{-2}$ found by Tai and Hodgkiss (1975) in eutrophic Plover Cove Reservoir in Hong Kong. However, there do not appear to be definite increases in diatom numbers with eutrophication. Temporary ponds on Baffin Island, for instance, support populations of up to 1.6×10^8 cells cm $^{-2}$ (Moore, 1974). Douglas (1958) studying a nutrient-poor English stream reported numbers of over 1×10^6 *Achnanthes* species alone.

Diatom cell volume measurements more accurately describe diatom density. Small species, for instance, would not greatly increase a sample's diatom volume but would increase cell numbers. In Kootenay Lake average cell volumes are highest near the lake surface (Fig. 38, 40). These large diatoms, often possessing jelly stalks, are better able to remain attached and maintain an aqueous environment when subjected to wave action or exposed by altered lake levels (Patrick, 1948). Absolute cell volumes of between 0.5-4 mm^3 cm^{-2} of rock surface in Kootenay Lake are less than most diatom volumes in Baffin Island ponds (Moore, 1974) where standing crops reached 218.99 mm^3 cm^{-2}. Volumes did compare well with volumes ranging from 0.3-10 mm^3 cm^{-2} navigation buoys immersed for 145 days in Lake Winnepeg (Evans and Stockner, 1972). Obviously much more data is needed before diatom volumes can accurately be related to trophic conditions.

Algal diversity has often been used as a measure of water quality. Stresses caused by toxic wastes result in reductions in the numbers of species as well as in other diversity measures (Cairns and Lanza, 1972). Hohn (1961) noted that the introduction of highly toxic pollutants resulted in the reduction in diatom diversity, the degree of reduction being dependent upon the severity of the pollutant. Besch, Ricard, and Cantin (1972) confirmed that reductions in the numbers of diatom species occurred in the Northwest Miramichi River in New Brunswick as a result of mining (primarily zinc and copper) pollution. Williams and Mount (1965) observed reductions in algal diversity with additions of zinc, and Cairns et al. (1973) also observed lowered diversities in polluted systems.

The effects of eutrophication on algal diversity are more complex,

except in the zone of initial influence of sewage discharges etc., where deoxygenation reduces diversity. Williams (1964, 1972), for instance, in a study of United States rivers concludes that eutrophic stations were generally less diverse than "clean" stations. In a paleolimnological study of Lake Washington, Stockner and Benson (1967) found that diversity decreased with eutrophication. However, in a study of Lake Ontario's sediments, Duthie and Sreenivasa (1972) observed that diatom diversity did not decrease with eutrophication. Apparently, enrichment of waters does not always stress aquatic systems to the point where diversity is decreased. Krebs (1972) even states that high productivity is sometimes considered necessary for high diversities. Archibald (1972) argues that though severely polluted waters have low diversities, clean waters can have diversities ranging from high to low as a result of enrivonmental factors other than pollution which affect the structure of a community. A great deal of care is obviously needed in the interpretation of this parameter.

Shannon-Wiener diversities of about 2.5 - 3.5 within Kootenay Lake (Fig. 42) were certainly well above values of 1.0 which Weber (1973) considers indicative of polluted waters. Values in the north arm of the lake were generally higher than in the south arm. Though this pattern agrees well with previous measures of the algal community indicating the "cleaner" nature of the north arm, the diversity variations may be coincidental, as even south arm values were high. Indeed, there were no regional differences in the total numbers of species (Fig. 43), although there were more common species (making up 5 percent or more of the total diatom abundance) in the north arm of the lake.

Cluster analysis, using diatom data from all stations and depths, grouped together ecologically related areas of Kootenay Lake. These station grouping were remarkably similar to qualitative separations previously made using biomass, production and other types of attached algae data. North arm and south arm stations, which received vastly different phosphate loadings, separated into two distinct groups (Fig. 45, 46). Vertical comparisons supported the distinctiveness of the upper splash zone algal community compared to algal populations at the 3.0 and 5.0 m depths.

Diatom species (and other types of algae) have long been used as indicators of specific water types. Although the physiological requirements of many species are not known, a large number of quantitative distributional studies do relate diatom species to various amounts of nutrients and pollutants. Problems with the use of indicator species occur, as some researchers have 'overanalyzed' their data, designating quantitatively unimportant species as indicator organisms. The frequent occurrence of abnormal cells in some species (Cholnoky-Pfannkuche, 1971) can cause misidentifications and also confuse the literature.

In this study, only diatoms that were dominant in yearly average data (rather than in single samples) were used to form conclusions about water quality. This procedure should select the most reliable information on species distributions and, by the bulk of cells involved, is likely to minimize problems associated with incorrect identifications. Even with this procedure, 34 species were dominant at a minimum of one station in yearly average samples. Analysis of these 34 species distributions has the potential to produce many conclusions about the water quality and the supportive evidence

of all the indicators further minimizes problems related to possible misidentifications.

Perhaps my greatest safeguard against making incorrect species indicator assessments was Kootenay Lake's phosphate gradient, which acts as a built-in control. Other than this phosphate gradient, attached algae in the north and south arms of the lake are exposed to very similar conditions, which are not likely to influence the between station algal variations. However, in interpreting the algal distributions, more care is needed when comparing main lake algae to west arm algae, the west arm having a more lotic environment as well as domestic sewage inputs. Reciprocal transfer experiments strengthen conclusions made about the nutrient preferences of the diatom species. Decreases or increases in species abundancies after the transfers can be quantified and related to the particular species' environmental preferences, based upon Kootenay Lake distributional data and literature reports.

Kootenay Lake's diatom flora is dominated by alkaliphilic species commonly exhibiting eurytopic or eutrophic nutrient preferences. Nevertheless there are several distinct diatom distributional patterns indicative of specific regional or depthwise conditions within the lake (Fig. 47-50).

Algal assemblages in the splash zone of the main section of Kootenay Lake, for instance, were dominated by species able to withstand exposure and turbulence. Diatoms at the lake surface, characterized by *Cymbella* sp. A and *Gomphonema herculeanum*, were larger than those found at other depths. This large size and the presence of gelatinous secretions are the main adaptations enabling them to withstand the physical stresses.

The lack of regional variations in the main lake for these two species further indicates that they are primarily adapted to physical stresses rather than to nutrient levels. The *Cymbella* species is, as yet, unidentified and comparisons with other systems cannot be made. *Gomphonema herculeanum*, however, not only grows in the eutrophic south arm of Kootenay Lake but is also dominant in ultra oligotrophic but turbulent Lake Tahoe (Goldman, 1974) further confirming the species' adaptations to physical stresses and its wide nutrient tolerances.

Diatom patterns indicate that the splash zone of Kootenay Lake's west arm is significantly different from that of the main lake. Species tolerant of physical stresses are virtually absent from the west arm of the lake. Instead, the diatom assemblage more closely resembles those found at deeper west arm locations. These data conform to other evidence that the west arm is smaller, more protected and less subject to wind and wave action. Furthermore, diatoms from the west arm shoreline are typical planktonic species rather than attached forms. These species, characterized by *Asterionella formosa*, *Fragilaria crotonensis*, *Melosira varians* and *Stephanodiscus astraea*, probably originated from the pelagic regions of the main lake and began settling to the bottom once the water entered the river-like west arm. These "west arm" species typically dominate eutrophic waters (Brown and Austin, 1973; Gasse, 1974b; Golowin, 1968; Haworth, 1972; Palmer, 1969; Patrick, 1948; Patrick and Reimer, 1966; Stockner, 1972; Stockner and Benson, 1967; Whitton, 1974), although some of these species are also considered eurytopic (Duthie and Sreenivasa, 1972; Stoermer, Taylor, and Callender, 1971; Turoboyski, 1973), and *Fragilaria crotonensis* can even be

dominant in some oligotrophic lakes (Goldman, 1974; Patrick and Reimer, 1966). However, the possible transport of these species from the main lake prevents the west arm from being described as eutrophic.

The ubiquitous occurrence of a few species underlies some basic lakewide similarities, despite varying phosphate levels and physical stresses. *Achnanthes minutissima*, for instance, is equally common in all three major lake regions, perhaps responding to similar alkalinities and similar levels of several other chemical constituents and physical parameters such as temperature and energy inputs. *Achnanthes minutissima* appears to be an indicator of temperate waters in general (Besch et al., 1972; Brown and Austin, 1973; Castenholz, 1960; Douglass, 1958; Ennis, 1975; Foged, 1954; Godward, 1937; Schoeman, 1972; Stockner and Armstrong, 1971), only disappearing where toxic or anoxic conditions prevail (Besch et al., 1972; Schoeman, 1972). Its widespread distribution within Kootenay Lake perhaps attestifies to a generally healthy, non-toxic (even if eutrophic) environment. The *Nitzschia* species complex, making up about 5 percent of the diatom population at all stations, can be related to relatively low and evenly dispersed nitrogen levels within the lake. The *Nitzschia* abundancies in Kootenay Lake are certainly well below dominance levels of at least 50 percent associated with high nitrogen levels from sewage plant outfalls (Schoeman, 1972).

Species exhibiting distributional gradients in the north and south arms have the most potential as indicators of phosphorus-produced eutrophication. *Fragilaria vaucheriae* best represents the group of species which grow optimally in the north arm, barely tolerating the south arm of the lake and its high inputs of phosphorus. This species is reported as being

eurytopic to mesotrophic in distribution (Foged, 1954; Stoermer et al., 1971). Reciprocal transfer experiments confirm that *F. vaucheriae* achieved its highest dominance levels in the north arm rather than in the phosphate rich south arm.

The increased abundance of *Fragilaria construens* (and varieties) in regions of high phosphate loadings, at all depths, suggests the species' value as an indicator organism. Indeed, the species has generally been associated with eutrophication in other lakes (Gasse, 1974a,b; Hunding, 1971; Richardson and Richardson, 1972; Stockner and Benson, 1967), although there are some reports from oligotrophic and mesotrophic lakes also (Patrick and Reimer, 1966; Schoeman, 1972). The transfer experiments produced the most conclusive evidence of the value of *F. construens* as an indicator of high phosphorus levels. Whether initially grown in the north, south or west arms it usually showed negative competitive responses (occasionally very minor positive responses) when transferred to the more oligotrophic north arm (Fig. 51). Alternatively, the increase in *F. construens* dominance when transferred to the south arm region of high phosphate loadings (Fig. 51) further reinforces the species' value as an indicator of phosphorus enrichment.

CONCLUSION

The trophic classification of major regions within Kootenay Lake, based upon inshore phosphorus concentrations, would result in false impressions about the lake's water quality. Consistent regional variations in concentrations of dissolved orthophosphorus, total dissolved phosphorus or total insoluble phosphorus were not apparent, despite large differences in loadings to the north and south arms of Kootenay Lake. Calculations based upon phosphate supplies necessary to sustain the attached algal growth rates show that attached algae remove large amounts of phosphorus from the water. This fact could partly account for the insufficiency of chemical data alone to detect regional variations in the lake's trophic conditions. Furthermore, extractions of surplus stored phosphorus from the attached algae reveal that algae near areas of highest phosphate loadings contain much more stored phosphorus than do algae in other regions of the lake.

In contrast to the phosphorus results, Kootenay Lake's attached algae exhibit regional variations. Resultant conclusions about water quality variations within the lake do conform to expected patterns, considering the differences in phosphate loadings to major regions of the lake. The south arm, a region of the high phosphate loading, has the highest amount of excess phosphorus storage, algal abundance and production, results being comparable to those obtained in several eutrophic waters. In contrast, the north arm algae store less phosphorus, are less abundant, have lower growth rates, and are more typical of mesotrophic and oligotrophic waters. Many of the green algal and diatom species identified in the south arm are considered to be

eutrophic indicators. Moreover, these species are generally absent or less common in other areas of Kootenay Lake. Diatom diversities were high throughout the lake, perhaps reflecting a healthy, even if enriched environment. Diatom cluster analyses delineated the lake into subregions, confirming the distinctiveness of the north, south and west arms and thereby adding supportive evidence on the attached algal based trophic classifications within Kootenay Lake.

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